LYNX (FELIS LYNX) BIOLOGY AND MANAGEMENT: A
LITERATURE REVIEW AND ANNOTATED BIBLIOGRAPHY

LYNX (*Felis lynx*)

BIOLOGY AND MANAGEMENT

A LITERATURE REVIEW
AND
ANNOTATED BIBLIOGRAPHY

Prepared for the U.S. Forest Service

Northern Region
Threatened, Endangered, and Sensitive Program

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PART I   LYNX BIOLOGY AND MANAGEMENT SUMMARY

INTRODUCTION

This document summarizes information on the biology and management of
the Canada lynx (*Felis lynx*) and presents a bibliography of current
literature.   The primary emphasis is management of the lynx in the
United States south of Canada, therefore a priority for review and
inclusion has been placed on literature concerning lynx in this area,
secondly on literature concerning lynx in Canada and Alaska, and
finally, on work deemed relevant from Europe and Asia.   Lynx are
dependant to a great extent on the status of their primary prey, the
snowshoe hare (*Lepus americanus*), therefore significant literature
concerning the management of snowshoe hares and their habitat is
included in the bibliography.

The literature review was conducted using several computer data bases
such as BIOSIS, the Fish and Wildlife Reference Service Database, and
several libraries.   In addition, a letter requesting information on
current and recent lynx studies was sent to Wildlife Cooperative
Research Units, state wildlife agencies, Canadian provincial ministries
of environment, and state Natural Heritage Programs in states and
provinces where lynx occur.

TAXONOMY

Felis lynx Linnaeus, 1758

Order Carnivora, Family Felidae, Subfamily Felinae, Genus *Felis*, Species *lynx*

Common names: Canada lynx, lynx, gray wildcat, gray lynx, link, lucivee, *loup-cervier* (French Canadian), *pichu* (French Canadian), *lynx boreal* (French), *Luchs* (German)

There is considerable debate about specific classification of the wild cats. The lynx is now generally considered one circumpolar species with several distinct subspecies. See Jones et.al. (1986), McCord and Cardoza (1982) and Tumlison (1987) for further discussion and references. Some current literature, and many older sources, refer to the North American lynx as *Lynx canadensis*.

DESCRIPTION

The lynx is a medium-sized cat, the largest of the bob-tailed cats, with long legs, a short, compact body, a flared facial ruff, and prominent black tufts (4-5 cm long) on its ears. Sexes are similarly colored. Winter pelage is generally a grizzled or yellow gray color; summer pelage is shorter, and browner (Jackson 1961, Saunders 1961).

Juveniles are a pale buff, spotted or streaked with brown or black (Jackson 1961). Color variations in lynx are rare, though Jones (1923) reported "fawn yellow", "drab blue", "light brown", and "tabby" variations.

The tip of the lynx tail is completely encircled in black, whereas the bobcat (*Felis rufus*) tail is black only on the dorsal surface.

Lynx vary in size depending on sex and geographic locality. Males are generally about 33% larger than females. Nearctic lynxes ranged from 4.5 to 17.3 kg (Nava 1970, Saunders 1961, 1964, van Zyll de Jong 1963). Palearctic lynxes are larger than Nearctic lynxes. Male lynx averaged 17.9 kg in a study conducted in Sweden (Haglund 1966).

Lengths of Nearctic lynx males in Alaska ranged from 71 to 85 cm, and females were 67 to 82 cm (Nava 1970). Newfoundland lynx were somewhat larger. Males ranged from 73.7 to 106.7 cm, and females from 76.2 to 96.5 cm in length (Saunders 1961).

Lynxes are digitigrade, with sharp retractile claws. There are four toes on the hind feet, and five on the larger front feet, although the fifth toe is raised and may not show in the track (McCord and Cardoza 1982).

The permanent dental formula for adult lynx is i 3/3, c 1/1, p 2/2, m 1/1, total= 28, and the deciduous dental formula is i 3/3, c 1/1, p

2/2, m 0/0 (Van Zyll de Jong 1963).

DISTRIBUTION

The presumed ancestor of the lynx originated in Africa in the early to middle Pliocene, migrating throughout the northern hemisphere by the middle Villafranchian (Tumlison 1987). The now extinct Lynx issiodorensis was holarctic in distribution by the middle Pleistocene, and probably gave rise to the modern lynx, Felis lynx lynx and F.l. canadensis (Kurten and Anderson 1980).

The modern lynx is holarctic in distribution. It is widespread through the boreal regions of North America, Europe and Asia, but its distribution has been considerably reduced in the United States and western Europe (McCord and Cardoza 1982, Tumlison 1987). In Eurasia it is still found in timbered areas from Scandanavia eastward through Siberia, and locally in Mongolia, western and northern China, southeastern Tibet, upper India and Pakistan, Manchuria, Korea, parts of Iran and Iraq, the Carpathians and the Caucasus, Poland, Czechoslavia, Yugoslavia, Rumania, and Greece, and rarely in the western Pyranees of France (Guggisberg 1975, Tumlison 1987). A disjunct and endangered population (F.l. pardina) is found in southern Spain (McCord and Cardoza 1982).

In North America the lynx are found in forested areas on mainland

Alaska except the panhandle and Seward peninsula (Manville and Young 1965), and across Canada from the Yukon and central British Columbia eastward to Quebec, Labrador,and Newfoundland (Banfield 1974). Lynx are also found in northern New England (Godin 1977, Litvaitis et al. 1987), portions of the Lake States (Jackson 1961, Gunderson 1978), the Rocky Mountains south to Colorado (Rust 1946, Idaho; Hoffman et al. 1969, Montana; Armstrong 1972, Colorado; Reeve et al. 1986, Wyoming; and McKay 1991, Utah), and in restricted localities in Washington and Oregon, including the North Cascades (Ingles 1947, Nellis 1971).

Much of the literature on distribution of lynx documents rare or unusual occurances outside of its normal range (Schorger 1947, Wisconsin; Schantz 1947, Nevada; Erickson 1955, Michigan; Doll et al. 1957, Wisconsin; Harger 1965, Michigan; Coggins 1969, Oregon).

Preliminary distribution maps for lynx have been prepared by a committee of the Interagency Lynx/Wolveriine/Fisher Working Group. The maps, for the states of Colorado, Idaho, Montana, Oregon, Utah, Washington, and Wyoming, are included here in Figures 2 through 8. Figure 1 is the cover letter for these distribution maps citing references and other information used to develop these preliminary maps. Note that the overall strategy for compiling the maps was to draw a line around all records, both current and historical, irrespective of verification, from Natural Heritage Program data bases, state records, and other published distribution data.

Figure 1. Cover letter regarding distribution maps.

<div align="center">

Wolverine/Fisher/Lynx
Summary of Distribution Information

April 1, 1992
Prepared by M.Maj and Dr. Oz Garton

</div>

The following is a summary of information that went into the development of the distribution maps (prelimi-
nary) of the wolverine, lynx and fisher for the states of California, Colorado, Idaho, Montana, Oregon, Utah,
Washington and Wyoming. The following summary is presented by individual states and species.
The overall strategy was to broadly draw a line around all individual records provided from Natural Heritage
Data bases, State records and published data and depict as distribution. No differentiation of historic versus
current records were made. All records were used irrespective of their verification.

The next version of distirbution maps will distinguish between current data (1982-1992) and historic data
(1981-older). Only verified and probable siting records will be used. Sign such as tracks and scat will not be
used. Enclosed is a version of the new distribution maps, fisher distribution in Oregon.

Total records; 1,001 wolverine records, 434 lynx records and 273 fisher records. totally 1608.

CALIFORNIA: No records

COLORADO: Lynx information from Halfpenny, Bissell, and
Nead 1982
143 records

IDAHO: Information from GAP analysis from University of
Idaho and Idaho Natural Heritage Program
1 record

MONTANA: Information from "Distribution of Montana
Amphibians, Reptiles, and Mammals" by Larry S.
Thompson 1982.

OREGON: Data from Nellis 1971 and Natural Heritage Program
database
11 records

UTAH: Information from Robin McKay, Natural Heritage
Program
9 confirmed, 8 possible records

WASHINGTON: Information from Brittell et al. 1989

WYOMING: Data from Wyoming Natural Heritage Program
database
262 records
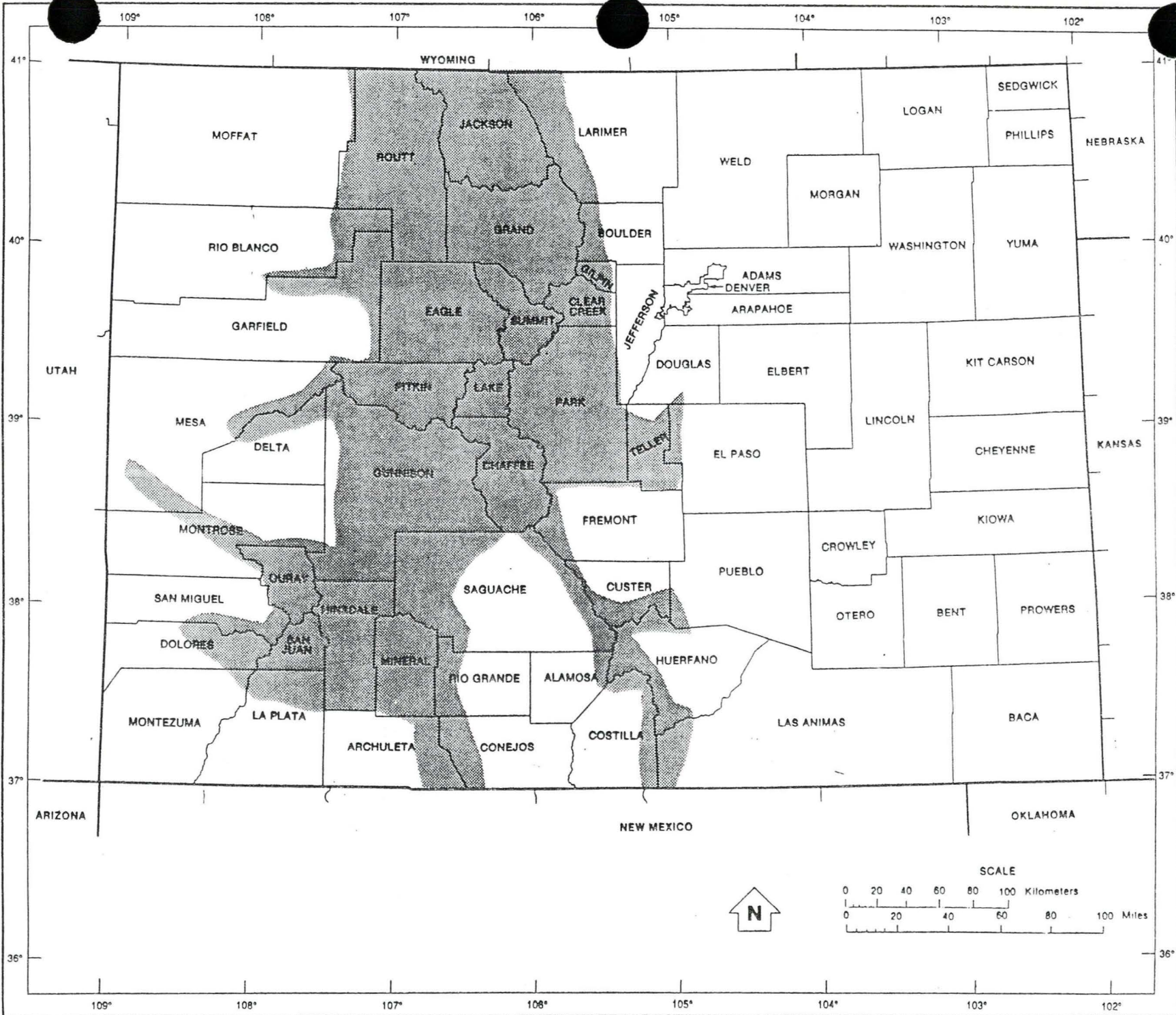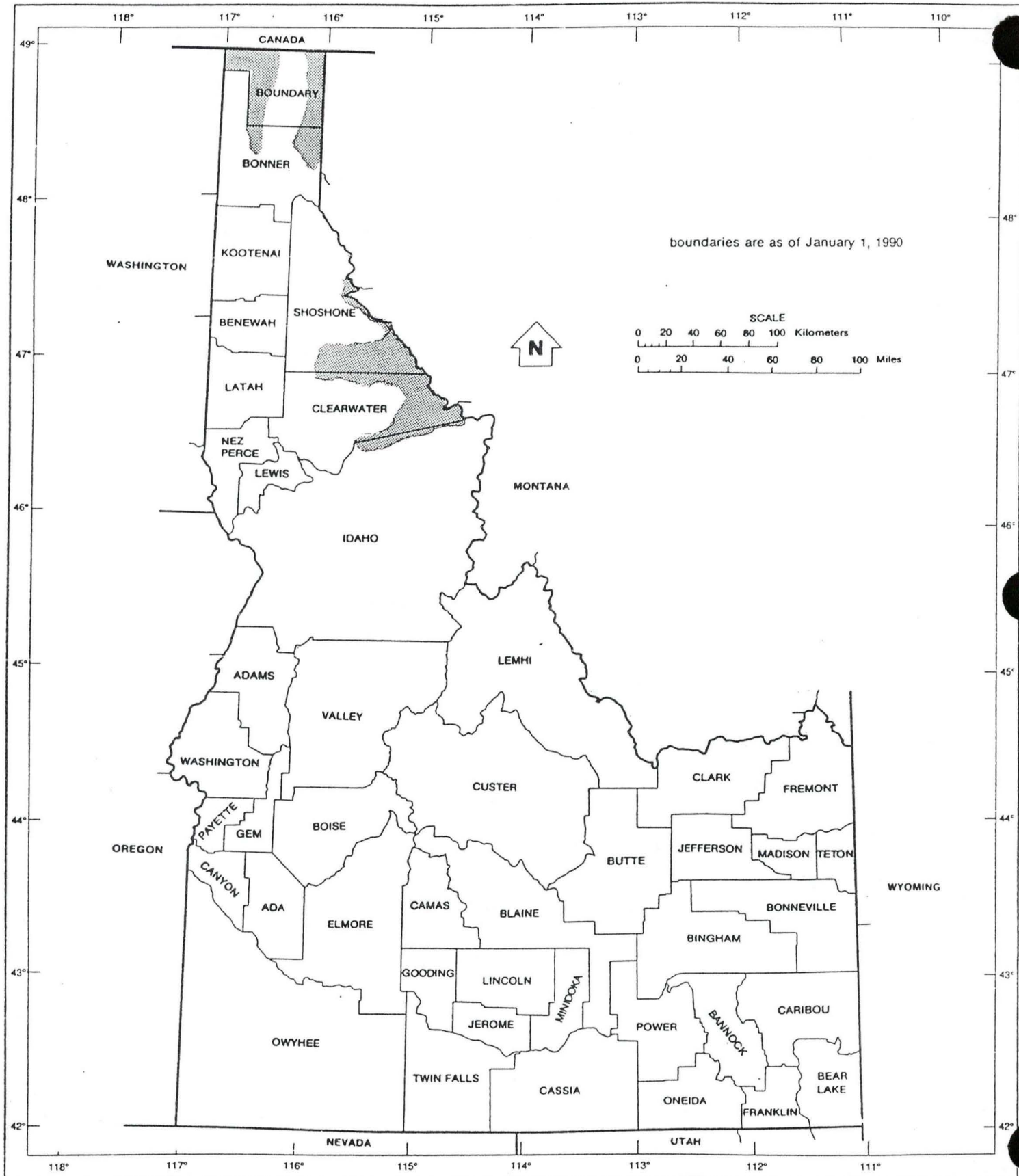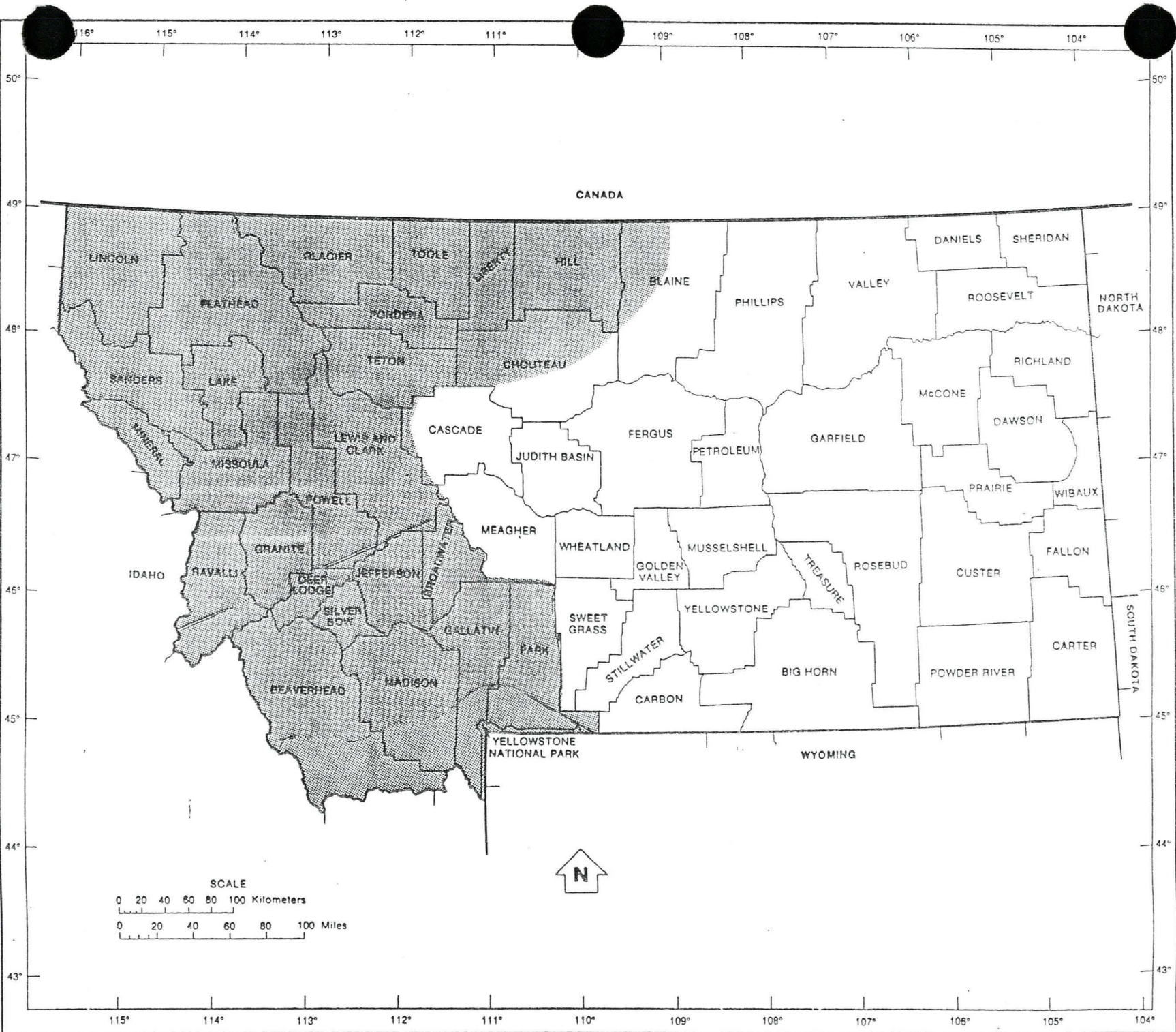
LYNX DISTRIBUTION

LYNX
DISTRIBUTION

Counties

boundaries are as of January 1, 1990

SCALE

U.S. DEPARTMENT OF COMMERCE   Economics and Statistics Administration   Bureau of the Census

MAPS

FIGURE 3:

IDAHO

LYNX DISTRIBUTION

CANADA

LINCOLN
GLACIER
TOOLE
LIBERTY
HILL
BLAINE
DANIELS
SHERIDAN
PHILLIPS
VALLEY
ROOSEVELT
NORTH DAKOTA
FLATHEAD
PONDERA
TETON
CHOUTEAU
RICHLAND
McCONE
DAWSON
SANDERS
LAKE
CASCADE
FERGUS
PETROLEUM
GARFIELD
MINERAL
LEWIS AND CLARK
JUDITH BASIN
PRAIRIE
WIBAUX
MISSOULA
POWELL
MEAGHER
WHEATLAND
MUSSELSHELL
TREASURE
ROSEBUD
FALLON
GRANITE
GOLDEN VALLEY
CUSTER
IDAHO
RAVALLI
DEER LODGE
JEFFERSON
BROADWATER
STILLWATER
YELLOWSTONE
SILVER BOW
GALLATIN
PARK
BIG HORN
POWDER RIVER
CARTER
SWEET GRASS
BEAVERHEAD
MADISON
CARBON
SOUTH DAKOTA
YELLOWSTONE NATIONAL PARK
WYOMING

N

SCALE
0 20 40 60 80 100 Kilometers
0 20 40 60 80 100 Miles

MAPS

FIGURE 4:   MONTANA

LYNX
DISTRIBUTION

FIGURE 5:   OREGON

LYNX
DISTRIBUTION

Counties

FIGURE 6:   UTAH

LYNX
DISTRIBUTION

FIGURE   7:   WASHINGTON

CANADA

WHATCOM

SAN JUAN

SKAGIT

ISLAND

CLALLAM

OKANOGAN

FERRY

STEVENS

PEND
OREILLE

SNOHOMISH

CHELAN

JEFFERSON

KITSAP

DOUGLAS

LINCOLN

SPOKANE

KING

MASON

IDAHO

GRAYS HARBOR

KITTITAS

GRANT

PIERCE

THURSTON

ADAMS

WHITMAN

LEWIS

PACIFIC

YAKIMA

FRANKLIN

GARFIELD

WAHKIAKUM

COWLITZ

SKAMANIA

BENTON

WALLA WALLA

COLUMBIA

ASOTIN

CLARK

KLICKITAT

OREGON

SCALE

0   20   40   60   80   100 Kilometers

0   20   40   60   80   100 Miles

N

LYNX DISTRIBUTION

Figure 8:

WYOMING

MONTANA

SHERIDAN

BIG HORN

PARK

CROOK

CAMPBELL

SOUTH DAKOTA

TETON

JOHNSON

WASHAKIE

WESTON

IDAHO

HOT SPRINGS

FREMONT

NATRONA

CONVERSE

NIOBRARA

SUBLETTE

NEBRASKA

LINCOLN

PLATTE

GOSHEN

SWEETWATER

CARBON

ALBANY

UINTA

LARAMIE

UTAH

COLORADO

SCALE

0 20 40 60 80 100 Kilometers

0   20   40   60   80   100 Miles

N

A revised version of these maps is currently (1992) being prepared by the committee that will distinguish between current data (1982-1992) and historic data (1981 or older) and will use only verified and probable sighting records.

LIFE HISTORY

Reproduction

The breeding season of the lynx may occur between January and May, depending upon latitude, longitude, altitude, climate, photoperiod, and perhaps prey availability (McCord and Cardoza 1982). Spanish lynx bred as early as January (Guggisberg 1975), while Palearctic lynx generally bred in February and March (Haglund 1966). Mating took place in March and April in Alaska (Nava 1970), between early March and early April in Newfoundland (Saunders 1961), and in April and May in Alberta (Nellis et al. 1972).

Male lynx probably do not breed until their second year (Saunders 1961, Stewart 1973). Females can breed by 10 months (Nava 1970), but may not breed until 22-23 months old (Saunders 1961, Van Zyll de Jong 1963). O'Connor (1982) reported that the age of first breeding and the proportion of females breeding varied in response to prey densities, peaking during the first spring following hare abundance. Delayed sexual maturity resulting from prey scarcity was also reported by Nava

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(1970) and Brand and Keith (1979).

Females may seek out males, and actively drive other females away. Courtship lasts 3 or 4 days, during which copulation occurs frequently (Rue 1981). Conception rates vary depending on prey availability. During years of high snowshoe hare density in Alberta, 73% of adult females conceived, but only 33% did when hares were scarce (Brand and Keith 1979). Age of first ovulation also appears to depend upon prey availability. Following hare population declines over a two year period in Alaska, 10-month old female ovulation rates declined from 99% to 10% (O'Connor 1982).

The lynx is presumed by some researchers to be a spontaneous ovulator, and can recycle up to three times if not bred, though there is some dispute on this point (McCord and Cardoza 1982, Quinn and Parker 1987).

The gestation period of lynx is about 9 weeks (McCord and Cardoza 1972). Seton (1929) reported a range of 60-65 days. Saunders (1961) estimated 63-70 days for wild lynx in Newfoundland. Parturition takes place in May or June (Saunders 1961, Nava 1970).

Litter sizes vary from one to six (Tumlison 1987). North American litters are usually three or four kits (Saunders 1961, Nava 1970, Brand and Keith 1979), though yearling females tend to have smaller litters, and individuals in these litters may be smaller (Brand and Keith 1971). One litter per year is considered normal for lynx, though some

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individuals may breed only in alternate years (Saunders 1961).

Lynx kittens are born with their eyes closed, ears folded, poorly developed ear tufts, and no teeth (Tumlison 1987). They are well furred, with dark brown longitudinal streaking on the back and limbs, and lighter streaking on the flanks (Saunders 1964), that fades until they acheive adult pelage between two (McCord and Cardoza 1982) and nine months of age (Jackson 1961). Eyes open between 10 and 17 days after birth (Tumlison 1987). They begin to walk at 24 to 30 days (Tumlison 1987), and are weaned by 12 weeks (McCord and Cardoza 1982). Tooth eruption begins with the lacteal canines at about 17 days, followed by the incisors, then the premolars (Van Zyll de Jong 1963, Tumlison 1987). Permanent dentition begins replacement around four months (Saunders 1961).

The litter remains with the mother until the next breeding season (Tumlison 1987).

Natality

Lynx are capable of producing up to five kittens (Berrie 1975) annually. Though placental scar counts and litter size varies depending upon prey abundance (O'Connor 1984, Hatler 1989), litters of two or three kittens are possible when hare numbers are low (Parker et al. 1983, Stephenson 1986), and four or five when hares are abundant (Berrie 1974, Brand et al. 1976). Average lynx litter sizes during low,

medium, and high hare densities all were near the overall average of 2.77 for 26 litters reported in five studies (Hatler 1989).

Yearling lynx are capable of reproduction, but O'Connor (1984), using histological evidence from a large sample gathered over one complete hare cycle, noted a 17.3-fold difference in productivity (recent placental scars) among yearlings between high and low hare abundance.

Hatler (1989), citing Nellis (1972) and Brand et al. (1976), noted that, during a 10 year study that took place through one complete hare cycle, they recorded *no* adults with litters during four years of low hare abundance (17 observations), 19% with litters during two years of intermediate/decreasing hare abundance (21 observations), and 59% with litters during two years of increasing or high hare abundance (22 observations). "Clearly," Hatler (1989) emphasized, "it is the absence of litters in several winters, not the size of the litters when they were present, that is of major importance in the context of long-term recruitment."

Mortality

Starvation is probably the dominant mortality factor for kittens, and often for juveniles, and adults (McCord and Cardoza 1982, Quinn and Parker 1987). Trapping pressure can be a major cause of juvenile and adult mortality, especially during cyclic lows (Berrie 1973, Brand and Keith 1979, Bailey et al. 1976, Quinn and Parker 1987). There is no

evidence that other factors play an important role in lynx mortality, though malnutrition may predispose lynx to diseases and parasites (Quinn and Parker 1987).

Though wolves (*Canis lupus*) may kill lynx if caught in the open (Banfield 1974), the major predator upon lynx may be other lynx (Quinn and Parker 1987), as infanticide appears to be commonly practiced among many carnivores.

Lynxes rarely survive past 15 years in the wild, though they have lived 22 years in captivity (Tumlison 1987).

Parasites and diseases

Lynxes are not known to have succumbed to epizootics due to heavy parasitic infections, and are presumed less vulnerable to this type of mortality than many mammals because of their solitary nature and their habit of changing denning and resting sites frequently (McCord and Cardoza 1982).

Ectoparasites documented on lynx by Van Zyll de Jong (1966b) included eight species of fleas, mostly common rodent fleas, and a louse. Internal parasites include tapeworms, roundworms, flukes, and spiny-headed worms (McCord and Cardoza 1982). The cestode *Taenia laticollis* and the roundworm *Toxascaris leonina* were found in 96% and 92% of the lynxes examined by Van Zyll de Jong (1966b), respectively.

Lynx are susceptible to feline distemper (panleukopenia) and rabies (McCord and Cardoza 1982).

ECOLOGY

Habitat

The lynx's selection of habitat is closely linked with the habitat requirements of its primary prey, the snowshoe hare (*Lepus americanus*) (Quinn and Parker 1987). Hare habitat characteristics and management have been described by Bider 1961, Keith and Windberg 1978, Wolfe et al. 1982, Peitz and Tester 1983, and Koehler 1990. In general, hares prefer mixed conifer stands for cover, with openings of shrubby hardwoods for feeding (Quinn and Parker 1987). Lynx use a wide variety of seral and climax coniferous and hardwood habitats (Hatler 1989). On Cape Breton Island in Nova Scotia, Parker (1981) found lynx highly selective of open conifer stands 22 to 28 years old in winter, avoiding mature hardwood stands and younger successional stands because of inadequate conifer cover. In Montana, Koehler et al. (1979) reported 90% of relocations of two radio-collared lynx were in dense, fire-created stands of lodgepole pine supporting a high snowshoe hare population. An Alaska report (ADFG 1987) stated that lynx preferred fire-produced mid-successional stands within large expanses of forest, and alpine shrub thickets.

Lynx use mature forest for denning and resting (Hatler 1989). Den

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sites are often in hollow logs or brush piles in dense thickets (McCord and Cardoza 1982). Daylight bedding sites are frequently in thickets near game trails (McCord and Cardoza 1982).

Home range

Reported home range sizes for lynx vary from 10 to 243 km2 (McCord and Cardoza 1982) but are normally 16 to 20 km2 (6-8 miles2) (Quinn and Parker 1987). Home range size depends upon sex, age, population density, prey density, and survey method (McCord and Cardoza 1982). Male lynxes have larger home range sizes than females (Quinn and Parker 1987). Large ranges may indicate sparsity of prey or other resources, and may reflect a relative absence of social interaction (Hatler 1989). Lynx home ranges increase with decreasing hare density, and they may abandon home ranges entirely, becoming nomadic below certain levels of hare abundance (Ward 1985, Ward and Krebs 1985).

Hatler (1989) pointed out that reported home range estimates are difficult to compare reliably because of differing survey methods, duration and intensity of studies, calculation methods, and differences in age, sex, density, and nutritional status of the study animals.

Daily movements

Lynx are generally more active at night, and more active when hungry than when well-fed (Quinn and Parker 1987). As most daily movements are

related to hunting, the amount of activity can be expected to vary with prey density and hunting success (Hatler 1989). The shortest observed distances between bedding sites was 1.0-1.8 km/day in Alberta (Nellis and Keith 1968) and 4.2 km/day in Newfoundland (Saunders 1963b). Several studies, using snow tracking or telemetry techniques, report average daily distances traveled of about 8 km (Saunders 1963b, Parker 1981, Stephenson 1986). The average distance traveled per day increased from 4.8 km to 8.8 km in Alberta in consecutive years (Nellis and Keith 1968), even though the hare density was increasing. They speculated that differences in hunting conditions (snow depth) the second year decreased success rates. Brand et al. (1976) reported average daily cruising distances ranging from 3.3 to 8.0 km and noted that distance traveled was directly related to hunting success, but neither hunting success or distance traveled was directly related to hare densities (Hatler 1989). Ward and Krebs (1985) documented lynx movements during a snowshoe hare population crash on their Yukon study area, and recorded a doubling of daily cruising radius. They speculated that studies finding no correlation between hare density and daily movements were not at hare population lows.

Dispersal behavior

Dispersal, as used here, refers to long range movements, including emigration and immigration, that may take an individual to a new range. Several authors have documented dramatic long range movements for lynx; 103 km (62 miles) for a juvenile female (Saunders 1963b), 164 km (98

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miles) for an injured adult male (Nellis and Wetmore 1969), 325 km (195 miles) for an adult female in Montana (Brainerd 1985), 250 km (150 miles) for a male and a female within the Yukon (Ward 1985), and 616 km (370 miles) for an adult male that dispersed north from Washington State to central British Columbia (Brittell et al. 1989). Transients are generally believed to be young animals in search of an unoccupied territory (Brittell et al. 1989), but adults may become transient if food resources are scarce (Ward and Krebs 1985, Brittell et al. 1989).

Territoriality

Do lynx maintain and defend areas for exclusive use? Study results to date demonstrate considerable variation in lynx maintenance of territory. The evidence suggests that at least under some conditions lynx do maintain territories. Working with captive animals, Lindemann (1955) reported that European lynx demonstrated a strong tendency to maintain a well-defined home range, marking the boundaries with urine and feces. Keith (1974) and Brittell (1987) both concluded that lynx behavior demonstrates social intolerance and mutual avoidance, these traits serving to separate them spatially and temporally.

Koehler (1987b) reported strong territoriality, with little overlap between sexes, and considerable overlap between. The findings of Mech (1980) and Stephenson (1986) were similar, except that the overlap among females ranged from slight to considerable.

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During a period of snowshoe hare decline in the Yukon, Ward and Krebs (1985) concluded that lynx were not territorial, having considerable overlap of range both within and between sexes. Nellis et al.(1972), Brand et al.(1976), and Carbyn and Patriquin (1983) all reported varying degrees of overlap between and/or within sexes.

It is probable that the size of a territory, and the degree that it is maintained and defended, is dependant upon the availability of resources within that area. Keith (1974) felt that there was little point in defending a territory containing insufficient resources. In areas with highly cyclic prey populations, there may also be little point in maintaining a territory with abundant resources. Conversely, in regions with fairly stable prey populations, the maintenance of territories may be advantageous. This interpretation would account for the strong territoriality exhibited on Koehler's (1987b) Washington study area, where the prey base is relatively varied and stable, the absence of territoriality in the Yukon, a region of great fluctuations in prey base (Ward and Krebs 1985), and the varying degrees of overlap between and within sexes reported by other studies, depending upon how cyclic the prey base was, and where in the cycle the study was undertaken.

POPULATION DYNAMICS

Cycles

Lynx populations display periodic numeric fluctuations, known as "cycles", occurring over a ten-year period (Quinn and Parker 1987). These cycles were first noticed in the early 1900's by biologists and mathematicians reviewing more than two hundred years of furbearer harvest records kept by the Hudson's Bay Company (Tumlison 1987). The definitive analysis and description of the cycle was presented by Elton and Nicholson (1942). They reported that "the cycle in lynx furs is very violent and regular and has persisted unchanged for (206 years). Its average period is about 9.6 years... the cycle is a real one in lynx populations."

Numerous causes for the lynx cycle have been proposed and supported or discounted in the literature, including sunspots, forest fires, prey availability, weather, logistic inconsistencies, mathematical anomolalies, lunar influences, trapping effort, and so on (see Elton and Nicholson 1942; Moran 1949; Cole 1951, 1954; Butler 1953; Wing 1953; Rowan 1954; Gilpin 1973; Archibald 1977; Arditi 1979; Finerty 1979; Winterhalder 1980). Current evidence suggests that lynx populations fluctuate dramatically because of their dependence on snowshoe hares, and that hare populations fluctuate due to an as yet incompletely understood "hare-vegetation interaction" (Keith 1974). Apparently hares become so numerous that their over-browsing decreases

quantity and quality of food supplies, leading to starvation (Quinn and
Parker 1987).   Population declines are a result of malnutrition and
predation (Keith et al. 1984).

As hare populations decline, lynx populations follow one or two years
later (McCord and Cardoza 1982).   Their populations "crash" primarily
because of decreased productivity of adult and yearling females, and
starvation of kittens (Quinn and Parker 1987).   Though lynx apparently
switch to alternate prey during these periods, they generally cannot
maintain a positive energy balance by doing so, and thus continue to
decline in physical and reproductive condition (Brand and Keith 1974).

Whether or not lynx and snowshoe hare populations are cyclic in the
lower United States is unclear.   Dolbeer and Clark (1975) suggest that
in many cases they are not, because lynx and hare habitat is fragmented
and disjunct.   Because of this, survival of dispersing hare juveniles
into sub-optimal habitat is low, and therefore populations remain
relatively stable.   Thompson (1987) suggests that it is unlikely that
lynx populations dependant upon hares would be cyclic if hares are not.

Density

The densities reported for lynx vary considerably across their range
and over time, depending on habitat conditions and food availability.
Quinn and Parker (1987) summarized a number of studies done in North

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America and Russia and concluded that most reported lynx densities fell in the range of 1 lynx/15-25km^2 (6-10miles^2). During periods of low hare abundance, reported densities are generally 2-4 lynx/100km^2 (Hatler 1989). The highest density reported for lynx during a population high was 20 lynx/100km^2 on Cape Breton Island, Nova Scotia (Parker et al 1983). Hatler (1989) pointed out that this unusually high density may be an artifact of the island situation and/or an unusual concentration in the particular habitats composing the small (60km^2) study area. Typically, lynx densities following hare population highs range from 5/100km^2 (Iurgenson 1955, Stephenson 1984) to 9/100km^2 (Brand et al 1976).

Lynx populations apparently are capable of greater than 4-fold increases between population lows and highs (Brand and Keith 1979), though reports in the literature of much greater increases are probably erroneous, and may have been based on harvest increases (Hatler 1989). A fourfold increase in lynx numbers in Alberta was accompanied by a 20-fold increase in harvest (Brand and Keith 1979).

Sex ratios

Reported sex ratios for lynx vary widely, ranging from 92 (Brand and Keith 1979) and 93 (Saunders 1961) males/100 females to 525 yearling males/100 yearling females (n=25) and 153 males/100 females of all age classes (n=96; Stewart 1973). The greater proportion of males generally reported has been attributed to a greater vulnerability of males to

trapping due to larger home range sizes and more vigorous breeding season activity, though McCord and Cardoza (1982) argue that both of these assumptions may not be accurate. Hatler (1989) suggested that the sex composition of lynx populations may vary with the stage of the cycle and/or harvest intensity. Modelling of theoretical populations have shown that small changes in sex ratio can substantially affect population growth (O'Connor et al 1987).

FOOD HABITS

The snowshoe hare (*Lepus americanus*) is the primary prey of the lynx throughout its North American range (Saunders 1963a, Nellis and Keith 1968, Brand and Keith 1979, Parker et al 1983, Koehler 1987b). The proportion of hares in the diet depends on hare availability. When hare densities were low, they comprised 43 percent of lynx diets in an Alberta study, and 100 percent during periods of hare abundance (Brand et al 1976). McCord and Cardoza (1982) stated that, based on scat and digestive tract analyses, hares made up 65 percent of the lynx spring diet, 52-91 percent in summer, 52-62 percent in fall, and 61-85 percent in winter. Other prey frequently used by lynx, especially during periods of lower hare abundance, are mice and voles (especially *Microtus* and *Clethrionomys*), red squirrels, grouse, and ptarmigan (McCord and Cardoza 1982, Hatler 1989). Only snowshoe hares can support high density lynx populations (Brand and Keith 1979).

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Depending upon density, lynx kill one or two hares every three days (Quinn and Parker 1987, Hatler 1989). Lynx will cache hares (Nellis and Keith 1968). Lynx have been known to attack whitetailed deer (Seton 1929), to occasionally consume the young of deer, caribou, and moose (Quinn and Parker 1987), and were demonstrated to be a major limiting factor on caribou herds in Newfoundland (Bergerud 1971). Other than in Newfoundland, lynx are not considered important predators of ungulates in North America (Quinn and Parker 1987).

The larger Eurasian lynx preys on hares and other small mammals (Haglund 1966, Pulliainen 1981), and apparently uses ungulates, especially roe deer (*Capreolus capreolus*), more frequently than its North American counterpart (Iurgenson 1955, Haglund 1966).

CURRENT STATUS

The lynx is currently listed as a Category 2 species by the U.S. Fish and Wildlife Service (C2= Taxa for which information now in possession of the Service indicates that proposing to list as endangered is possibly appropriate, but for which conclusive data on biological vulnerability and threat are not currently available). A petition to the Fish and Wildlife Service to list the species as threatened was filed in the North Cascades of Washington state within the past few years. A "no action" decision was taken in 1992.

The U.S. Forest Service lists the lynx as a sensitive species (the

Table 1. Status of the lynx by agency.

U.S. Forest Service		
	Region 1	S
	Region 2	S[*]
	Region 4	S
	Region 5	-
	Region 6	S

U.S. Fish and Wildlife Service	Category 2

Bureau of Land Management	S

State Agencies	
California	-
Colorado	E
Idaho	FB
Montana	FB
Oregon	-
Utah	P
Washington	GS
Wyoming	P

S = Sensitive
T = Threatened
NG= Nongame species
P = Protected species
FB= Furbearer
E = Endangered

S[*] = Proposed as sensitive

U.S. Forest Service define a sensitive species as one for which population viability is a concern as evidenced by significant current or predicted downward trends in population numbers or density, or habitat capability) in Regions 1, 4, and 6, and it is proposed as a sensitive species in Region 2 (Table 1).

The lynx is listed as a furbearer by the states of Idaho and Montana, a protected species in North and South Dakota, Oregon, and Wyoming, and Endangered in Colorado and Wisconsin (Table 1). Though technically listed as a "game species" in Washington, all legal harvest was terminated in 1991 pending a review of its status and possible listing by the state as threatened (Brittell, pers. comm.). The lynx is also listed as a "protected game animal" in Minnesota, but there has been no season since 1982, due to virtually no lynx in the state except for occassional dispersers from Canada (MN Div. of Wildl. personnel, pers. comm., Sept. 1992).

Idaho and Montana currently have lynx trapping seasons with limited quotas. The harvest in Idaho between 1973 and 1980 ranged between 7 and 39 lynx, by 1982 had dropped to 2, and there was only one lynx taken between 1982 and 1991 (data provided by the National Wildlife Federation). Montana harvests reached 300 during the 1972-1973 season, averaged 44 annually between 1977 and 1985, peaking during the 1983-1984 season at 69 lynx harvested. Since 1987 the annual harvest has steadily decreased (Hash 1990). The harvest in 1990-1991 was two lynx.

MANAGEMENT

Habitat management

The most comprehensive guidelines to maintain or improve lynx habitat have been developed by Brittell et al. (1989) and Koehler and Brittell (1991), both copied in the last section of this document, and both highly recommended reading for anyone interested in lynx habitat management. To summarize Koehler and Brittell's (1991) management recommendations:

Managing For Prey

. small diameter twigs and new growth (< 0.4in. diameter) are preferred browse in winter

. willows and birches, tips of conifers, bark all important winter hare food

. for browse saplings must be taller than snow depth, yet short enough to reach (where snow depths reach 3-4 feet, trees must be 6-8 feet tall

. security cover provided by dense stands 4690 - 13440 stems per acre (extremely dense stands of little use if understory sparse, stands of < 3000 stems per acre lack adequate security and thermal cover)

. Conifer essential as they offer more cover than hardwoods

. Hare habitat should be well dispersed - hares may not recolonize clearcuts until 6 - 7 years after cutting, and

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may not reach highest densities for 20 - 25 years

. Units designated as hare habitat should be greater than 20 - 25
acres

. Logging and thinning units less than 40 acres offer hares forage
and security

. During reforestation it is important to maintain naturally
occurring palatable shrubs and trees.

Managing For Denning

. Lynx need mature forest for denning

. downed logs and stumps may be most important component

. dispersed stands 1 - 5 acres of mature forest connected by trvwl
corridors needed to allow females to move kittens toward
more abundant prey and avoid disturbance

. Pockets of mature forest must be near prey habitats

Managing For Cover

. Lynx do not generally cross openings wider than 300 feet, but
will travel through silviculturally thinned stands with 180
trees per acre devoid of shrubs

. to minimize effects of logging and open areas on lynx, cutting
units should not be placed next to large meadows, burned
areas, or recent clearcuts

. cover should be maintained along ridges and saddles

. density of trees should be greater than 180 per acre and
clearcuts should be less than 300 feet wide or have

constrictions less than 300 feet wide to allow lynx to cross

Fires and Forest Management

. forest management should provide a temporal and spatial array
  of openings, early successional, and mature forests

. forest mangers should strive for a mixture of openings (natural
  and artificial) in stands of harvestable-sized timber while
  maintaining dispersed stands of mature forest

. natural wildfires and prescribed burns can provide early
  successional forests and temporal and spatial mosaics

. maintain patches of old-growth for denning

. schedule clearcuts, stand thinning, and prescribed burning to
  provide a balance of successional stages

. thinning and logging residue may require treatment to prevent
  competition with forbs and shrubs, but some residue should
  remain for small mammals, etc.

. diseases and insects can contribute to an open forest canopy,
  but may increase the chance of large wildfires

. herbicides should be applied, if at all, when there will be
  little adverse impact on browse for hares, and should be
  species specific

. roads should be kept to a minimum, and main roads should be kept
  primitive to mitigate effects of human disturbance, huning
  and trapping, and disruption of lynx travel and hunting
  patterns

. weeds, forbs, shrubs, and seedlings along roadways with less

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than 50 foot rights-of-way encourage lynx use and encourage
growth of hare forage

. construct deadend rather than loop roads to minimize public
disturbance

. roads should be closed once timber harvest is complete, with
physical barriers in place to ensure minimal disturbance

. cattle grazing may compete with hares for forage and should be
closely monitored

Table 2. Recommended Cover Ratios For Lynx Habitat (Brittell et al.
1989)

In primary lynx habitat zones;

denning cover	6%
travel corridors	30%
forage/thermal/	
hiding/stalking cover	30%
non-lynx cover	33%

(non-lynx cover includes grass-forb-shrub-seedling stand
categories and natural openings excluding water)

Population management

A predator such as the lynx, existing under the best of conditions in
relatively low densities, and prey dependant, cannot be "managed" in
the traditional sense used by wildlife managers using concepts such as

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"sustained yield" and "compensatory mortality" (Brittell et al. 1989).

Lynx are cyclic, as are their primary prey species, and during several

parts of the cycle recruitment is low to non-existent. Any mortality

under these conditions is additive rather than compensatory. Lynx

populations will decline whether harvested or not, but continually

harvested populations will decline further, and recovery will be slower

than will unharvested populations (Brand and Keith 1979). Furthermore,

lynx numbers at the peak are determined by the level at which recovery

began, and the length of time of recovery (Brittell et al. 1989).

Lynx are considered quite vulnerable to trapping under most conditions

(Burris 1971, van Zyll de Jong 1971, Bailey et al. 1986, Quinn and

Parker 1987), though evidence suggests this vulnerability varies with

sex and age class, and physical condition (Hatler 1988), and exposure

to trapping activities (Brittell et al. 1989, Anderson 1991).

Overexploitation and its effects have been documented by Berrie (1973)

and Bailey et al. (1986). "Overexploitation, particularly during the

critical low period, minimizes potential recovery, reduces the

expansion of dispersing lynx into vacated habitats, and jeopardizes

sub-populations in the more accessible areas " (Brittell et al. 1989).

A "tracking strategy" for lynx harvest management has been suggested by

Brand and Keith (1979), increasing harvest quotas during lynx

population peaks, and completely curtailing harvest during cyclic lows.

They recommend keeping track of population trends through analysis of

annual fur harvests; when kitten recruitment sharply drops a year or

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two after peak fur harvests, trapping should be curtailed for three or four years to allow lynx recovery. "To harvest from a population with essentially zero recruitment for 3- to 5-year periods is not sound management" (Quinn and Parker 1987).

Relying solely on harvest data to set seasons has some potential pitfalls. Long-term data from Alaska (O'Connor 1984) revealed that regional lynx populations peaked three years before harvest peaked, and reproductive performance declined up to four years before harvests declined. "Harvest trend alone does not accurately reflect population performance and trend" (Hatler 1988).

The minimum data-set necessary to manage lynx populations, according to Quinn and Parker (1987) includes:

1) the chronology of lynx harvest statistics and prevailing regulations relative to specific management regions;

2) the chronology of snowshoe hare abundance relative to specific management regions;

3) assessment of the above to evaluate the magnitude and temporal trends of the lynx-hare cycle;

4) annual samples of lynx carcasses (collected from trappers) to assess sex and age structure and fecundity;

5) results of (4) assessment relative to (1) and (2);

6) annual collection of winter lynx abundance indices from winter track transects or field personnel's impressions; and

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7) awareness by managers of all literature relative to lynx-hare cycles and an understanding of the principles that control lynx densities.

Lynx seasons generally center on the period of greatest pelt primeness in December and January (Hatler 1988). The sex and age composition of the harvest changes depending on whether the population is increasing, decreasing, or stable (Quinn and Parker 1987), and throughout the trapping season (Parker et al. 1983). Managers can potentially influence the composition of the harvest by timing of the trapping season. During years of high recruitment yearlings will constitute a high proportion of the harvest, especially earlier in the season (Quinn and Thompson 1985). Kittens generally show up in the harvest later in the season, and the proportion of adult males to adult females in the harvest is greater later in the season (Quinn and Parker 1987).

Alaska and much of Canada regulates the maximum harvest of lynx by controlling the length of the season (Hatler 1988). Quotas and bag limits are often used to limit total harvest, especially when populations are at low densities, or are near cyclic lows, and when much of the harvest is taken by a relatively low proportion of trappers (Hatler 1988).

Management of lynx populations in the "lower 48", that is, south of Canada, should be conservative "because of the animal's low numbers, limited distribution, restricted environments, years with little or no

reproduction, habitat loss, increased accessibility, and high demand by sportsmen for lynx pelts" (quoted from Brittell et al. 1989 in reference to Washington state, but appropriate for all states inhabited by lynx south of Canada). Brittell, et al. (1989), realizing that population densities and harvest levels in Washington are chronically too low to detect population trends without considerable expense of time and money, recommend a strategy allowing for a static harvest level acceptable during population lows, though overly conservative during high periods. They recommend a permit system, applying to all lynx harvest, with variable quotas and season dates depending on population status. The lynx season was closed to all harvest in late 1991, and remains so pending further investigation of its status in Washington (Brittell, pers. comm., Sept. 1992).

Techniques

Monitoring

Numerous techniques for surveying and monitoring of lynx have been developed. Often the cost, effectiveness, and applicability of these techniques has not been fully evaluated before being adopted. The Monitoring Committee of the Interagency Lynx-Wolverine-Fisher Working Group has been developing a dichotomous key to allow a user to select an appropriate method for surveying or monitoring lynx, depending upon the management objectives. It is the wish of the Working Group to promote the use of standardized techniques, and to see that they are used most effectively and efficiently.

The Monitoring Committee suggested that the selection of a detection device to be used in a monitoring program be 1) affordable, 2) able to verify with evidence, 3) easy to transport and establish, 4) standardized, and 5) simple to use by all cooperators.

Different levels of monitoring intensity were identified. These are:

Level of Monitoring Intensity

I   Presence or absence

II   Distribution

III   Population Trend

IV   Population Size

V   Population Composition

The Committee developed a list of monitoring techniques and listed their advantages and disadvantages for Level I monitoring for wolverines (Figure 9). It is the intent of the Committee to complete an analysis of these techniques and to analyze their costs for Levels I through IV for lynx, wolverine, and fisher, and to produce a manual outlining their recommendations, as well as producing training materials and workshops to disseminate this information.

Methods of monitoring lynx populations were discussed by Koehler and Brittell (1991). They suggested that snow track counts can be cost-effective, but it's reliability depends upon the trackers experience, the effect of snow and lighting on track visibility, the speed at which

Figure 9. Monitoring techniques.

IV. Level 1 - Wolverine.

Listed below are the techniques considered, in order of increasing dependence on sophisticated technology, for wolverines at Level 1.

Technique	Advantages	Disadvantages	Costs
1. *Incidental sightings* of individuals and their sign.	Low cost; Many observers; Large area covered; Good PR; Educational; Used at any season; Can ID areas for future work.	Sightings need verification; No control over effort; Limited to visitor use areas; Presence only-limited confidence in absence.	Posters; Brochures; Data entry; Training; Verification.
2. *Surveys:*			
a. *Snow track counts* (trained personnel who return with physical evidence; photo, measurements)	Reliable data on multiple species; Large area covered; Simple-few instruments/hardware; Flexibility of scheduling; Good data on absence.	Need adequate and proper snow cover; Labor intensive.	Transportation; Survival gear; personnel training; Additional gear- cameras tape, film, etc. Costs depend on mode of travel - foot, snowmobile, aircraft.
b. *Track-plate counts* (sooted and partially covered with contact paper; baited and enclosed in a "cubby")	Positive ID; Good pad print provides physical evidence from which accurate measurements can be collected; Bait and lure increases detections; Can be used all seasons and when access is best; Easy to schedule; Data on a number of species; Immediate ID not necessary.	No gait pattern; Limited to certain species; Bait/lure can alter behavior; repeat visits by personnel are necessary; More gear needed to transport and set-up; Non-target species can inactivate the station.	More than snow-tracks...(?)
c. *Hair snares* (baited cylinders of wire)	Provides physical evidence; Used during all seasons and by many species; Bait/lure increases detections; Technicians need not be too skilled; Immediate ID not necessary; Potential for genetic ID to species.	ID based on structural characteristics is difficult; Hair is infrequently snared; Bulky; Negative PR.	Similar to track-plate....
d. *Cameras*			
1. *"Low -tech"*; (110 print film; manual trigger)	Inexpensive; Can be used for other studies; Physical evidence and positive ID; Bait/lure increases detection; Used all seasons; Used when access is best; Ease of scheduling; May recognize individuals.	Vulnerable to weather; Relatively high failure rate; Small negative; Trigger requires that subject must pull bait; Non-target species inactivate the station; Limited to 1 photo per visit; Repeat visits necessary to service; Experience technicians necessary; No time/date on film.	Similar to track-plate...

the survey is conducted, and the influence of human activities on lynx movement. Track counts should be conducted several times each month along established routes and within an established time after last snowfall (Koehler and Brittell 1991).

Thompson and Halfpenny (1989) developed a system of classification for rating tracks and signs that may have originated from Canada lynx (Table 3). This classification allows a researcher to classify tracks as positive, probable, possible or negative lynx tracks.

Capture and immobilization

Occassionally the need arises to capture lynx, for instance to apply radio collars. Brittell et al. (1989) captured 25 lynx a total of 40 times in a Washington state study using box traps (42 X 15 X 20 inches, Tomahawk Live Trap Company and 48 X 32 X 24 inches) and modified No. 2 and 3 coilspring leghold traps. They reported that both methods frequently missed lynx. They had a higher trapping success with the leghold traps, but lynx initially sustained leg injuries until the traps were modified.

Captured lynx were immobilized using an intramusular injection of ketamine hydrochloride (Vetalar, Parke-Davis) in an estimated dose of 5 mg/pound of body weight (11mg/kg) (Brittell et al. 1989).

Though a number of immobilizing drugs, including succccinylcholine

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Table 3. Classification system for rating tracks and signs which may have originated from Canada lynx.

Category	Description

Positive

(1) Presence of signs which provide undisputable evidence, including skulls, skins, individual hairs, or clear, distinguishable tracks. Distinguishable tracks should be over 7.5 cm in width, and only shallowly sinking into the snow. Straddle should be greater than 15 cm, center straddle greater than 5.0 cm, and center stride from 60 to 70 cm. The leading edge of the print must form a flat arc and not show the stepped pattern found in canines.

(2) A combination of supporting evidence including a good track series and appropriate behavior indicated by the animal's trail. Appropriate behavior includes chases and kills of snowshoe hare, using all available cover and seldom crossing clearings. When crossing clearings, faster gaits, trots and lopes are used, travel from base to base of trees, dropping down into each tree well, moving through dense underbrush and small openings, investigating each snowshoe hare form, walking on top of snowshoe hare trails, and climbing trees requiring support from retractile claws. Other supporting evidence includes track location in appropriate habitat including spruce-fir forests and ecotones of spruce-fir, aspen and/or meadows, and presence of snowshoe hare sign.

(3) The majority of the signs must strongly indicate lynx with no significant contradictory clues.

Probable

(1) A combination of signs, the majority or best of which suggest lynx. Some clues may not fit the criteria for lynx, but none of these clues should strongly suggest other animals; the clues just simply aren't conclusive. Usually clues which do not suggest lynx fail to do so because the signs are in poor condition and difficult to interpret. A marginal measurement for one or two criteria can be out-weighed by the bulk of other clues. Measurements of straddle and print width are the two most distinguishing characteristics of the trail patterns and should be indicative of lynx if they are visible.

Possible

(1) A combination of signs, most of which indicate lynx. However, one or two clues may suggest, but not prove, another animal. If tracks are unclear, the totality of their sign should suggest lynx, but one or two types of measurements in a series might not be of appropriate size. Most attention should be paid to straddle and print width. Tracks seen at a distance and including a clear, wide straddle and print width, but not investigated should be classified as possible.

Negative

(1) A combination of signs, the totality of which indicate that the animal is not a lynx. A single clear clue of several indicative clues may be used to rule out a lynx classification.

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chloride, phencycladine, and PHC-promazine have been used to restrain and handle lynx and bobcat, ketamine hydrochloride is now the preferred drug for immobilization, as it has a wide margin of safety, does not relax skeletal muscles, and permits normal pharyngolaryngeal reflexes (McCord and Cardoza 1982). Suggested dosage ranges from 5.5 to 21 mg/kg estimated body weight (McCord and Cardoza 1982). Addition of acepromazine induces muscle relaxation but may induce hypothermia or apnea. Excessive salivation may be reduced with atropine (McCord and Cardoza 1982).

Age determination

The age of lynx can best be determined by examining tooth replacement in kittens, canine teeth for an open apical foramen in juveniles, and cemenatum analysis for adults (McCord and Cardoza 1982). Saunders (1964) reported that the apical foramen in canines of lynx closed between 13 and 18 months of age. Analysis of stained and sectioned teeth for deposition of cementum annuli has been used successfully to age older lynx in a number of studies (Nellis et al. 1972, Crowe 1972, Brand and Keith 1979). Nellis et al. (1972) have verified age determination using this method with known age lynx.

PART II LYNX LITERATURE

There have been surprisingly few comprehensive lynx bibliographies published in the past: Grundy 1964, Sweeney and Poelker 1977, Hatler 1988, and McKay 1991. Hatler is by far the most useful, containing most recent citations, including most of the pertinent papers with information on life history and management of the species, and an excellent subject index.

Any comprehensive attempt to review and comment on the literature has to have some boundaries, and often these are subjective. Grundy (1964) was a partial bibliography of the lynx, Sweeney and Poelker (1977) was an annotated bibliography and literature survey. Hatler (1988) focused on North American literature, especially that relevant to life history and management, as well as everything published on the lynx in British Columbia. McKay (1991) included some of the classic literature and everything pertaining to the lynx in Utah that she could locate.

This work focuses on management of the lynx in the contiguous United States, primarily in the mountainous west. The bibliography is divided into four parts:

I. Bibliography

This section includes every title that pertained to the biology and management of the lynx in the western United States, excluding Alaska. Because the majority of extensive field work has been done in Canada and Alaska, literature from these areas is referenced when it provided valuable information on the life history or management of the species. Some of the classic literature from Eurasia has also been referenced, especially if it contains new or more in-depth information than that available in North

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America, was generally obtainable in the United States or Canada, and had at least an English summary.

An abbreviated keyword follows each citation in **bold.**

KEYWORDS
behav- behavior, foraging behavior
biblio- bibliography
cycles- cycles
descript- description
distrib- distribution
ecol- ecology
food- food habits
habitat- habitat
hares- hares
harv- harvest
hist **distrib**- historical distribution
homerng- home range
mgt- management
mgt tech- management techniques
mort- mortality
para/dis- parasites and diseases
pop- population
reprod- reproduction
status- status
taxon- taxonomy

II. Subject Index

An index of topics referenced by keyword to each bibliographic citation is included here.

III. Annotated Bibliography

Papers that I judged were fairly important contributions to the literature, including classic field studies, in-depth literature reviews, and studies directly pertaining to the management of lynx in the western United States were included in this section. As Hatler (1989) and McKay (1991) had previously annotated much of this literature, I have used their annotations where possible.

Hatler (1989) listed the citation, followed by three alphabetical codes, and comments. The codes he used are: A) a significance rating of 0-3, with 0 rated as insignificant and 3 as very significant; B) geographic area considered in the paper; and C) a short description of the contents of the paper. All annotations from Hatler (1989) are noted with an asteric (*). Annotations from McKay (1991) are marked with two asterics (**) before the citation.

PART III. Papers

Copies of the papers I judged most significant to the biology and management of the lynx are included in their entirety in this section.

LYNX (*Felis lynx*) LITERATURE REVIEW

001   Adams, A.W. 1963. The lynx explosion. North Dakota Outdoors
      26:20-24.
      distrib

002   Adams, L. 1959. An analysis of a population of snowshoe hares
      in northwestern Montana. Ecol. Monogr. 29:141-170.
      hares

003   ADFG. 1987. Report to the Board on lynx management. Alaska Dep.
      Fish and Game, Div. of Game, Juneau. 30pp.
      mgt

004   Anderson, C. 1991. Lynx capture and marking study in the Vail
      area. Progress report, CO Div. Wildl.
      distrib, mgt tech

005   Archibald, H.L. 1977. Is the 10-year wildlife cycle induced by
      a lunar cycle? Wildl. Soc. Bull. 5:126-129.
      cycles

006   Arditi, R. 1979. Relation of the canadian lynx cycle to a
      combination of weather variables: a stepwise multiple
      regression analysis. Oecologia 41:219-233.
      cycles

007   Armstrong, D.H. 1972. Distribution of mammals in Colorado.
      Mono. Mus. Nat. Hist., Univ. Kansas. 3:297-298.
      distrib

008   Bailey, T.N. 1971. Immobilization of bobcats, coyotes, and
      badgers with phencyclidine hydrochloride. J. Wildl. Manage.
      35:847-849.
      mgt tech

009   Bailey, T.N. 1981. Factors influencing furbearer populations
      and harvest on the Kenai National Moose Range, Alaska. *In* J.A.
      Chapman and D. Pursley (eds.) Proc. Worldwd. Furbearer Conf.,
      Frostburg, MD.
      harvest, habitat, pop

010   Bailey, T.N. and E.E. Bangs. 1983. The significance of natural
        sanctuaries in maintaining lynx population levels on the Kenai
        National Wildlife Refuge. In S.W. Buskirk (ed.), Abstracts of
        Pap. Pres., Third Northern Furbearer Conf., Univ. Alaska,
        Fairbanks.
        harvest, pop

011   Bailey, T.N., E.E. Bangs, M.F. Portner, J.C. Malloy, and R.J.
        McAvinchey. 1986. An apparent overharvested lynx population on
        the Kenai Peninsula, Alaska. J. Wildl. Manage. 50:279-290.
        harvest, mort, pop

012   Bailey, T.N., E.E. Bangs, M.F. Portner, T.V. Schumacher, and
        M.B. Kesterson. 1987. Response of lynx to management changes
        on the Kenai National Wildlife Refuge, Alaska, 1984-1987. In B.
        Townsend (ed.). Abstracts of Pap. Pres., Fourth Northern
        Furbearer Conf., Alaska Fish and Game, Juneau.
        harvest, mgt

013   Banfield, A.W.F. 1974. The mammals of Canada. Univ. Toronto
        Press, Toronto.
        descript, distrib

014   Bangs, O. 1897. Notes on the lynxes of eastern North America,
        with descriptions of two new species. Proc. Biol. Soc.
        Washington.   11:47-51.
        descrpt, distrib

015   Barash, D.P. 1971. Cooperative hunting in the lynx. J. Mammal.
        52:480.
        behav

016   Barnes, C.T. 1927. Utah mammals. Bull. Univ. Utah 17:43.
        descript, distrib

017   Beale, D.M., and A.D. Smith. 1973. Mortality of pronghorn
        antelope fawns in western Utah. J. Wildl. Manage. 37:342-352.
        food

018   Bergerud, A.T. 1971. The population dynamics of Newfoundland
        caribou.   Wildl. Monogr. 25:1-55.
        food

019   Berrie, P.M. 1972. Sex differences in response to phencyclidine
       hydrochloride in lynx. J. Wildl. Manage. 36:994-996.
       mgt tech

020   Berrie, P.M. 1973. Ecology and status of the lynx in interior
       Alaska. The world's cats 1:4-41.
       habitat, homerng, pop

021   Bider, J.R. 1961. An ecological study of the hare *Lepus
       americanus*. Can. J. Zool. 39:81-103.
       hares

022   Brainerd, S.M. 1985. Reproductive ecology of bobcats and lynx
       in   western Montana. M.S. Thesis, Univ. Montana, Missoula.
       85pp.
       reprod

023   Brand, C.J., and L.B. Keith. 1979. Lynx demography during a
       snowshoe hare decline in Alberta. J. Wildl. Manage. 43:827-849.
       harvest, food, mort, pop

024   Brand, C.J., L.B. Keith, and C.A. Fischer. 1976. Lynx responses
       to changing snowshoe hare densities in central Alberta. J.
       Wildl. Manage. 40:416-428.
       food, homerng, mort, pop

025   Breitenmoser, U. and H. Haller. 1987. Feeding ecology of the
       lynx (*Lynx lynx*) in the Swiss Alps. Saeugetierkd 52:168-191 (In
       German, English summary).
       food

026   Brittell, J.D. 1987. Social behavior of lynx (*Felis lynx*) in
       Washington. In B. Townsend (ed.). Abstracts of Pap. Pres.,
       Fourth Northern Furbearer Conf., Alaska Dept. Fish and Game,
       Juneau.
       behav

027   Brittell, J.D., G.M. Koehler, R.J. Poelker, and S.J. Sweeney.
       1989. Native cats of Washington. WA Dept. Wildl., Olympia.
       169pp.
       distrib, harvest, mgt, pop

028   Brocke, R.H., K.A. Gustafson, and A.R. Major. 1990. Restoration
        of lynx in New York: biopolitical lessons. Trans. North Am.
        Wildl. Nat. Resour. Conf. 55. Pp.590-598.
        distrib

029   Brooks, A. 1909. The lynxes of British Columbia. Forest and
        Stream 72:412.
        descript, distrib

030   Bulmer, M.G. 1974. A statistical analysis of the 10-year cycle
        in Can. J. Anim. Ecol. 43:701-718.
        cycles

031   Bulmer, M.G. 1975. Phase relations in the ten-year cycle. J.
        Anim.Ecol. 44:611-620.
        cycles

032   Burris, O. 1971. Lynx management in Alaska. Pp.30-33 *in*
        Jorgenson, S.E., and L.D. Mech, *eds*. Proc. symp. native cats of
        North Am. U.S. Fish and Wildl. Serv., Twin Cities, MN. 139pp.
        habitat, harvest, mgt

033   Bursey, C.C., and M.D.B. Burt. 1970. *Taenia macrocystis*
        (Diesing, 1850), its occurrence in eastern Canada and
        Maine,U.S.A., and its life cycle in wild felines (*Lynx rufus*
        and *L. canadensis*) and hares (*Lepus americanus*). Can J. Zool.
        48:1287-1293.
        para/dis

034   Butler, L. 1942. Fur cycles and conservation. Trans. North Am.
        Wildl. Conf. 7:463-472.
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       behav, habitat, food

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        behav, homerng

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        food

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       habitat, harvest

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        habitat

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        distrib

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      mgt

226   Thompson, R.W., and J.H. Halfpenny. 1989. Canada lynx presence
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      mgt, pop

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      cycles, harvest

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      descript

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      distrib, taxon

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        ecol, homerng, mort, pop

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        behav, food, pop

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        harvest, mgt

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        behav, food, pop

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        Annual Prog. Rep., Furbearer Manage. Prog., Yukon Dep.
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        hist distrib, taxon

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        cycles

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        2:28-51.
        cycles

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        Ojibwa hunting and trapping practices. Am. Nat. 115:870-879.
        cycles, harvest

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      Snowshoe hare cover relationships in northern Utah. J. Wildl.
      Manage. 46:662-670.
      hares

254   Wolff, J.O. 1980. The role of habitat patchiness in the
      population dynamics of snowshoe hares. Biol. Monogr. 50:111-
      130.
      hares

KEYWORDS

Each citation in the Literature Review is followed by one or more
keywords. These keywords refer to topics featured in that reference.
The list is not exhaustive; for instance, information on population
cycles may be found in other references than those noted, and topics
other than cycles may well be covered in a citation followed by the
keyword cycles. This is simply an effort to help the reader begin to
locate the key works on a given topic.

The following lists each reference in the Literature Review that
features the topic of interest.

behav (behavior)
   15,26,38,44,63,64,81,83,90,91,103,109,117,118,
   125,132,137,138,145,149,163,164,165,174,175,179,182,189,192,194196
   ,206,231,232,241,242,244

biblio (bibliography)
   80,94,147,220

cycles
   05,06,30,31,34,35,37,45,49,60,62,65,66,70,72,112,113,115,133,
   157,158,159,190,210,230,249,250,251,252

descript (description)
   13,14,16,29,41,52,53,54,84,87,88,99,102,107,109,
   135,152,166,181,198,203,213,223

distrib (distribution)
   01,04,07,13,14,16,27,28,29,36,41,42,43,48,50,51,52,53,55,57,59,67,
   69,79,81,82,85,86,87,88,89,92,98,99,100,102,104,111,
   135,140,142,143,147,148,154,162,165,166,186,188,193,199,201,203,
   212,224,226,227,234,240

ecol (ecology)
   41,44,63,81,103,110,119,120,175,182,189,192,195,204,206,229,231236

food
   17,18,23,24,25,97,132,136,160,174,180,185,197,204,218,219,237,
   241,242,244,248

habitat
   09,20,32,59,61,106,124,126,174,185,215,223

hares
   02,21,56,114,115,116,122,124,139,151,176,177,185,253,254

harvest
   09,10,11,12,23,27,32,50,52,53,62,75,167,183,184,209,215,230,243246
   ,252

hist distrib (historical distribution)
   46, 128,144,153,188,247

homerng (homerange)
   20,24,38,118,126,196,236

mgt (management)
   03,12,27,32,39,58,68,71,72,73,74,77,78,93,94,111,123,124,127,
   136,145,167,170,179,182,191,207,225,228,229,232,239,243,245,246

mgt tech (management techniques)
   04,08,19,36,47,61,84,131,154,156,171,172,202,214,216,217   ,

mort (mortality)
   11,23,24,105,120,133,145,195,236

para/dis (parasites and diseases)
   33,40,134,141,178,200,211,238

pop (population)
   09,10,11,20,23,24,27,37,59,63,68,75,101,113,117,118,119,121
   132,145,162,169,170,175,182,183,184,195,209,221,222,228,231,236
   241,242,244

reprod (reproduction)
   22,95,96,130,150,161,168,169,205,219

status
   42,55,76,85,86,92,93,98,111,127,140,146,173,187,208,212,222
   226,227,239,245

80

taxon (taxonomy)
   46,51,88,108,129,155,234,235,240,247

ANNOTATED BIBLIOGRAPHY

Annotated bibliographies of a number of important papers on lynx biology and management are included here. David Hatler (Hatler 1988) and Robin McKay (McKay 1991) have given their kind permission to select and copy from the excellent annotated bibliographies that they have compiled. Hatler's annotations are marked with (*) and McKay's with (**).

Hatler (1988) listed the citation, followed by three alphabetical codes, and comments. The codes he used are: A) a significance rating of 0-3, with 0 rated as insignificant and 3 as very significant; B) geographic area considered in the paper; and C) a short description of the contents of the paper.

* ADFG. 1987. Report to the Board of Game on lynx management. Alaska Dep. Fish and Game, Div. of Game, Juneau. 30pp. (Provided by R.O. Stephenson).

Description - distribution
Habitat Characteristics - vegetation, cover.
Life History - lifehist.
Population Dynamics - poptrend.
Species Management - harvest, harv/strategy.
Habitat Management - fire, other/impacts.
Comments - This is an excellent review of the social, economic, and biological aspects that combine to create the current concern for lynx management throughout the species' North American range--failure of the law of diminishing returns because of high pelt prices, hence continued trapping pressure during cyclic lows, is a major contributor to the problem as it exists in the 1980's; as elsewhere, lynx are generally cyclic in Alaska, following the hare cycle by 1-2 years, but the cycle is not in synchrony statewide; as elsewhere, peak harvest during the early 1980's was less than in 1960's and 1970's. although that may not be due entirely to effects of trapping mortality--there is evidence of lower hare peaks in the 1980's in at least some areas; other relevant changes in Alaska in recent decades include a declining economy (making high lynx pelt prices increasingly attractive as a source of income supplement), increases both in general population and in the number of trappers, improved access through expanded networks of roads and increased use of snowmobiles and ATV's, and increasingly effective forest fire suppression; the two broad habitats of greatest importance to lynx are 1) "mid-successional vegetation stages" in large expanses of mixed forest "...in which fore governs habitat diversity..." and 2) alpine shrub thickets near timberline where "...snowshoe hare and other small game populations appear to be either not cyclic or not in phase with cycles in forested lowlands, thus providing lynx with food during periods of food scarcity elsewhere..."; the pros and cons of several different harvest management options are discussed--it is concluded that the presently most practical strategy is manipulation of seasons rather than methods and means, bag limits, or quotas: a tracking strategy, with greatest restrictions when lynx populations and recruitment are low, is recommended, but leaving at least some opportunity for harvest at that time in all but the most accessible units; parameters to be monitored in relation to the setting of regulations include trapping pressure, percentage of kittens in the harvest, and measures of levels and trends of lynx and hare populations; current lynx regulations and management strategies in Canadian jurisdictions are briefly reviewed, for perspective.

* Bailey, T.N. 1981. Factors influencing furbearer populations and harvest on the Kenai National Moose Range, Alaska. Pages 249-272 *in* J.A. Chapman and D. Pursley (eds.). Worldwide furbearer conference proceedings, Aug. 3-11, 1980, Frostburg, Maryland.

Population Dynamics - poptrend.
Species Management - harvest, harv/strategy.
Habitat Management - fire.
Comments - It is speculated that wildfires on the refuge may have caused declines in lynx numbers initially, but resulted in long-term gains through benefits to snowshoe hares; increasing harvest pressure on lynx during the low in the cycle is documented; a "tracking" harvest strategy, possibly monitored by population indices of snowshoe hares, is recommended.

✶ Bailey, T.N., and E.E. Bangs. 1983. The significance of natural sanctuaries in maintaining lynx population levels on the Kenai National Wildlife Refuge. *In* S.W. Buskirk (ed.). Abstracts of Pap. Pres., Third Northern Furbearer Conf., 22-23 March 1983, Univ. of Alaska, Fairbanks.

A) 3; B) Alaska; C) Radio-tracking and analysis of harvest data.
Population Dynamics - poptrend.
Species Management - harvest.
Comments - Abstract only: most of the biological investigations suggested in this preliminary report were expanded and results presented in subsequent papers, summarized below; an important point here is that most lynx were being caught in remote rather than accessible areas during the population low of the early 1980's, suggesting that "...naturally well-protected areas, or sanctuaries, are significant in maintaining the refuge's lynx populations" by supporting core populations that provide dispersing animals to the accessible, more heavily trapped areas.

✶ Bailey, T.N., E.E. Bangs, M. R. Portner, J.C. Malloy, and R.J. McAvinchey. 1986. An apparent overexploited lynx population on the Kenai Peninsula, Alaska. J. Wildl. Manage. 50: 279-289.

010   A) 3; B) Alaska; C) Radio-tracking 12 animals, assessment of hare densities, and examination of carcasses from trappers.

Habitat Characteristics - study/area, vegetation.
Life History - hmrange, movements.
Population Dynamics - natality, mortality, poptrend, popcomp.
Species Management - economics, harvest, harv/strategy.
Habitat Management - fire.
Comments - In response to increasing pelt prices, and with long (4 to 4.5 months) seasons and no limitations on numbers or distribution of trappers and trapping pressure, lynx were apparently overexploited on the Kenai National Wildlife Refuge (KNWR) in the 1970's; the harvest in 1971-74 (572) was almost 6-fold larger than that in 1981-84 (99), despite a more than 60% increase in number of documented trappers in the early 1980's; most lynx taken in the late 1970's and early 1980's were in less accessible and lower quality habitat, and with lower trapping effort; although two old males, aged 10 and 12 years, were taken from relatively remote areas, the average age of trapped animals ranged from 1.9 (30 males) to 2.3 (31 females); mortality of radio-collared animals increased from 44% to 86% between 1982-83 and 1983-84, and was 90% over the 2 year period; the dramatically lower

amplitude lynx cycle, as telemetry and snow tracking studies, occurred despite an increase of hares to estimated local densities of over 1000/km² in 1983 and 1984; based on observed trapping mortality of the radio-collared animals, juveniles were 5 times as vulnerable to trapping as adults, and males were twice as vulnerable as females; following continued harvest during the cyclic low, estimated densities of lynx on the KNWR during the increase and high phases of the hare cycle in the late 1970's and early 1980's (1.0/100 km² overall, and up to 2.3/100 km² in the highest quality habitat) were comparable to those documented during hare lows elsewhere; highest snowshoe hare use and apparent densities were in a 1947 burn, followed by alder-dominated and 1969-burned habitats, while mature forests showed the lowest use; despite high prey abundance, lynx home ranges were fairly large (50 and 89 km² for two females with young, and 64 and 783 km² for two adult males--on average the female ranges were less in summer (25 km²) than in winter (49 km²); continued increase in pelt prices insure continued interest in harvesting lynx--in 1984-85 the most accessible (northern) region of the KNWR was closed to lynx trapping by emergency order, the lynx season throughout the Kenai Peninsula was reduced from 120 to 47 days, and to reduce the incidence of "accidental" catches, cubby, bait, and flag sets commonly used for other species were prohibited in both the lynx closure area and in other areas during the closed season.

* Bailey, T.N., E.E. Bangs, M.F. Portner, T.V. Schumacher, and M.B. Kesterson. 1987. Response of lynx to management changes on the Kenai National Wildlife Refuge, Alaska, 1984-87. *In* B. Townsend (ed.). Abstracts of Pap. Pres., Fourth Northern Furbearer Conference, 3-4 April 1987, Alaska Dep. Fish and Game, Juneau.

A) 3; B) Alaska; C) Radio-tracking, 22 lynx, March 1984-February 1987.
Population Dynamics - mortality, poptrend.
Species Management - harv/strategy.
Comments - Abstract only: This study compared results for 13 lynx in an area closed to trapping, and 9 in an area with an open, but reduced season; 8 of 10 mortalities were from trapping, 1 from vehicle collision, and 1 unknown; mortality was reduced and local population density appeared to be increasing in the closed area, while mortality was greater and density apparently decreasing in the open area.

* Bergerud, A.T. 1971. The population dynamics of the Newfoundland caribou. Wildl. Monogr. 25. 55pp.

A) 2; B) Newfoundland; C) Long-term (10-year) study of caribou.
Life History - food.
Species Management - economics, harv/strategy.
Comments - It was concluded that lynx predation on newborn calves was "...the primary limiting factor..." in two major caribou herds, occurring primarily during lows in the snowshoe hare cycle.

✶ Berrie, P.M. 1972. Sex differences in response to phencycladine hydrochloride in lynx. J. Wildl. Manage. 36: 994-996.

A) 2; B) Alaska; C) Capture/handling phase of field study.
Species Management - field/tech.
Comments - Males were immobilized almost twice as long as females by a given dose of the drug, although long-term detrimental effects were not evident.

✶ Berrie, P.M. 1974. Ecology and status of the lynx in interior Alaska. Pages 4-41 *in* R.L. Eaton (ed.). The world's cats. Vol. 1. World Wildl. Safari, Winston, Oregon.

A) 2; B) Alaska; C) Radio-tracking, analysis of harvest records, necropsy of 3428 specimens obtained from trappers 1964-1970, trapper questionnaires, and trapper interviews.
Habitat Characteristics - study/area, vegetation.
Life History - hmrange, movements, denning.
Population Dynamics - natality, poptrend.
Species Management - field/tech, harvest, harv/strategy.
Comments - Home ranges of 14 to 25 km² were documented, although monitoring effort was not consistently applied; three apparent natal dens were found, two in spruce blow-down situations and one in "a tangle of washed up spruce roots" beside a creek--the last containing 5 kittens whose eyes had not yet fully opened (4 July 1970); in the harvest, as determined from carcasses purchased from trappers, males outnumbered females (about 60:40) in 2 of 3 years; the author postulated differential vulnerability of the sexes to trapping, but with seasonal differences-- his live-trapping efforts in summer netted 13

females and 1 male, while those in winter caught 1 female and 6 males; mean numbers of placental scars generally decreased from 1964-65 (5.01) through 1969-70 (3.60), but kits and yearlings increased in the harvest in the later years, especially in 1969-70; hares were believed at the low or slightly increasing at the start of the study period, and lynx were declining through 1966-67 and increasing thereafter; it is concluded that lynx survive primarily on small, local concentrations of hares during the low of the hare cycle, and that increased hunger and hunting activity at that time makes them more vulnerable to trapping; it is postulated that trapping during the low could result in a progressive decline in the cyclic amplitude, and a lynx trapping closure for up to 3 years during that time is recommended; it is noted that increase of human developments providing roads into wilderness areas, plus the advent of ATV's and snowmobiles, have greatly increased access for trappers to lynx refuge areas.

✶ Brand, C.J., and L.B. Keith. 1979. Lynx demography during a snowshoe hare decline in Alberta. J. Wildl. Manage. 43: 827-849.

A) 3; B) Alberta; C) Necropsy of 1108 carcasses, 1971/72 -1975/76.
Life History - food, nutrition, health.
Population Dynamics - natality, mortality, poptrend, popcomp, cycles.
Species Management - field/tech, economics, harvest, harv/strategy.
Comments - During the study period, hares declined on the Rochester study area from 388 to 5/100 ha, lynx on the study area declined from 13 to 0, and Alberta lynx fur sales

declined 12.5-fold; frequency of hare occurrence in stomachs decreased from 90% to 35% over the study period, while hare biomass declined from 97% to 65%--most alternative prey increased concurrent with lower hare consumption rates, but mice and voles comprised the only prey group whose frequency of use increased significantly (from 4% to 28%); increase in biomass due to increased use of mice and voles was negligible; indices of condition based on incidence of body fat indicated that trapped adults were usually in better condition than yearlings, that males were fatter than females, and that condition of all classes was poorest in late winters of low hare abundance; all reproductive parameters (ovulation and pregnancy rates and litter size as interpreted from placental scars) decreased as hares became scarcer; the sex ratio of the trapped sample was 48:52 in favor of females (n=974), but there were no significant sex differences within any age class or at different hare densities; mean age of the trapped sample rose from 1.6 years in 1971-72 to 3.6 years in 1975-76, as the proportion of kittens and yearlings decreased--however, there was evidence that kittens were under-represented in the sample, possibly because of care/protection provided by the adult female during the first winter; nevertheless, the estimated proportion of kittens in the population decreased from 66% to 3% between years of hare abundance and scarcity; estimated non-trapping mortality rates changed from 54-68% in 4 of 5 years (1965-67 and 1972-74), but was 34% in 1974-75--those rates and differences were not clearly related to spring population size; estimated trapping mortality averaged 10% of fall populations in 1965-67, but was 26% in 1971-75 (at similar population levels)--the

difference is speculated to have been due to higher pelt prices during the 1970's; within cycles, trapping mortality was density dependent (i.e., higher at higher population levels, and it appeared that trapping and non-trapping mortality were largely additive rather than compensatory; a "tracking" harvest strategy, with closures for about 3 years during the period of low/nil recruitment, is recommended; models of population increase under different management regimes show that the estimated Alberta population in the 1970's might have produced as many as 16 700 additional pelts (a 40% increase), despite 3 years of closure under a tracking strategy.

Brand, C.J., L. B. Keith, and C.A. Fischer. 1976. Lynx responses to changing snowshoe hare densities in central Alberta. J. Wildl. Manage. 40: 416-428.

A) 3; B) Alberta; C) Snow-tracking, 1964-68 and 1971-75.
Habitat Characteristics - study/area.
Life History - food, nutrition, activity, hmrange, socbehav, movements, health, behavior.
Population Dynamics - natality, poptrend, cycles.
Species Management - census.
Comments - Lynx densities were related to hare abundance, with a 1-year lag in population trends--numbers on the 130 km² Rochester study area ranged from 3 in 1966-67 (2.3/100 km²) to 13 in 1971-72 (10.0/km²); there were no kittens in the study area population in 1964-67 and in 1973-75, when hare densities were 137/100 ha or less, but there were 6, 7, and 4 kittens in 1967-68, 1971-72, and 1972-73, when hare densities were 185, 499, and

200/100 ha, respectively; home ranges of adults varied from 11.1 to 49.5 km², and range differences did not appear to be related to either lynx or hare density; two females with kittens had smaller ranges (mean 17.8 km²) than did six lone adults (31.5 km²); home ranges overlapped, thus the lynx did not appear to be strictly territorial, but there was some evidence of mutual avoidance, i.e., animals did not occupy the dame areas at the same time; snowshoe hare was the primary food, particularly in winter and during times of hare abundance--frequency of hare in the diet ranged from 38% during a winter of hare scarcity to 94% when hares were abundant; Ruffed Grouse and red squirrel were the numbers 2 and 3 food species in the winter samples, apparently taken opportunistically, while carrion was most used during the hare lows; summer foods were more variable, with slightly more occurrences of mice and voles than hares, although hare still predominated in terms of biomass; lynx were active mostly at night, and apparently spent most of their active periods in hunting;mean daily cruising distances, which varied from 3.0 to 8.8 km in different years, were related to kill success but neither distance travelled or kill success were clearly related to hare abundance; prey consumption rates of tracked lynx varied between 540-680 g (about 0.4-0.5 hare equivalents/day) when hares were abundant--although nutritional requirements were not known, it was concluded that the lower values may not have been sufficient to maintain free-ranging lynx in good condition, resulting in starvation-related losses to kittens and predisposition of adults to losses by trapping and encounters with humans in settled areas.

* Brittel, J.D. 1987. Social behavior of lynx (*Felis lynx*) in Washington. *In* B. Townsend (ed.). Abstracts of Pap. Pres., Fourth Northern Furbearer Conference, 3-4 April 1987, Alaska Dep. Fish and Game, Juneau.

A) 3; B) Washington; C) 40 live captures of 25 individual lynx, and radio-tracking, December 1980-October 1983.

Life History - hmrange, socbehav.

Population Dynamics - poptrend, popcomp, popreg.

Comments - Abstract only: The sex ratio of captured animals was 50:50; home ranges of residents did not differ between years or between sexes; mean home range size was 62.9 km² (males - 20.5 to 110.6 km²; females - 9.3 to 116.8 km²); the social organization of the studies lynx was believed to be similar to that for bobcats and cougars, involving social intolerance and mutual avoidance; it was concluded that the observed (estimated?) densities on the study area of 2.0 to 2.1 lynx/100 km² was the result of regulation by the social system.

Brittell, J.D., R.J. Poelker, S.J. Sweeney, and G.M. Koehler. 1989. Native cats of Washington. WAsh. Dept. of Wildl., Olympia. 169 pp.

This paper summarizes studies done in northcentral Washington to determine lynx ecology, habitat use, use of space, and survival rates. It also maps distribution od lynx in Washington, evaluates lynx harvest and monitoring programs, and makes habitat and population management recommendations for lynx in Washington. It includes a lliterature review of lynx.

Burris, O. 1971. Lynx management in Alaska. Pages 30-33 *in* S.E. Jorgensen and L.D. Mech (eds.). Symposium on the native cats of North America. U.S. Bur. Sports Fish. and Wildl., Fed. Bldg., Fort Snelling, Twin Cities, Minn.

A) 1; B) Alaska; C) Review of harvests and management/research activities.
Population Dynamics - natality, poptrend.
Species Management - economics, harvest, harv/strategy.
Habitat Management - fire, forestry.
Comments - Writing before the escalation of pelt prices in the late 1970's, the author believed that "...lynx harvests are related to population levels" and that "...low success by hunters and trappers in the years of low lynx populations will result in a self-regulating situation..."; it is noted that the most likely influence of humans on lynx populations would be indirect, through the effects of habitat changes on hare populations--especially fire suppression (believed negative) and logging (believed positive).

Carbyn, L.N., and D. Patriquin. 1983. Observations on home range sizes, movements and social organization of lynx, *Lynx canadensis*, in Riding Mountain National Park, Manitoba. Can. Field-Nat. 97: 262-267.

A) 2; B) Manitoba; C) Radio-tracking 3 animals, 1977-80.
Description - features.
Habitat Characteristics - study/area.
Life History - hmrange, socbehav, movements.
Population Dynamics - natality, mortality, poptrend.
Species Management - harvest, refuges.
Comments - The Manitoba lynx harvest peaked in 1978-79, thus this study probably involves the later stages of the increase phase of the cycle; the collared animals were two adult females (13.6 and 10.9 kg), each with two kittens when captured, and one adult male (15 kg); one female/young group travelled with two other animals, believed to be another adult female with one young, for 30 days; home ranges of the collared females over the November-February period were 138 km² and 177 km², while the 7.5-month range of the male was 221 km²; the female ranges overlapped, and there is evidence that the male's

range overlapped that of the females; all of 5 marked lynx from RMNP were eventually killed by trappers outside the park, the females within a matter of months--the park is not considered large enough to maintain a viable lynx population with trapping at the periphery; based on the observation of the two family groups traveling together, the potential for adoption of orphaned kittens is discussed.

De Vos, A., and S.E. Matel. 1952. The status of the lynx in Canada, 1920-1952. J. For. 50: 742-745.

A) 2; B) Canada; C) Consideration of lynx harvest data, by province and in Canada as a whole, 1920-1950.
Description - distribution.
Population Dynamics - poptrend, cycles.
Species Management - harvest.
Habitat Management - forestry, other/impacts.
Comments - Based on a 3-fold decrease in harvest between the 1920's and 1940's peaks, plus evidence of shrinking range in the south, the authors concluded that the species was decreasing in Canada; both overtrapping and habitat changes from logging and other clearing were implicated; the national and provincial harvest totals, including that in British Columbia, show similar patterns of cyclic amplitudes over the period studied; some early restrictions on lynx trapping are described: Saskatchewan - closure in 1946, with special permits for harvesting lynx instituted in 1948 and 1949; Manitoba - closure, August 1946 through November 1949, with trapping by permit thereafter; Ontario - closure for 1951-52 season.

Finerty, J.P. 1979. Cycles in Canadian lynx. Am. Nat. 114: 453-455.

A) 1; B) Canada; C) Critique of selected papers on the existence of the 10-year cycle in lynx.
Population Dynamics - cycles.
Comments - The author shows that in suggesting that the lynx cycle precedes the hare cycle in some cases, Gilpin (1973) failed to recognize that the cycle is not synchronous over the whole of Canada; he also presents evidence that Weinstein's (1977) explanations and concerns about lynx population data are not to be taken seriously.

Fox, J.F. 1978. Forest fires and the snowshoe hare-Canada lynx cycle. Oecologia 31: 349-374.

A) 3; B) Canada; C) Literature review and analysis of lynx fur returns in relation to forest fire and weather variables.
Habitat Characteristics - vegetation, climate.
Population Dynamics - cycles.
Habitat Management - fire, other/impacts.
Comments - The 10-year hare and lynx cycle is shown to be correlated, both in extent and

periodicity, with the frequency and extent of fires, which promote successional habitats in which hare populations may best subsist and grow; it is postulated that fires may be the primary controlling variable, and that precipitation (primarily winter snow characteristics) modifies the response of hares to the abundance of post-fire successional habitat; snow may be important in the extent to which it covers winter food and/or enables hares to browse higher; a "lull" in the lynx cycle (1929-1954) was not related to a similar lull in fires or precipitation factors, and may have been caused by overexploitation of lynx at that time; more recently, intensive fire suppression and subdivision of habitat by land development are correlated with reduced hare cycles in the northcentral United States; a review of the literature shows that population responses to successional changes have been documented for a variety of boreal forest herbivores whose food preferences and requirements overlap those of snowshoe hares.

* Gunderson, H.L. 1978. A midcontinent irruption of Canada lynx, 1962-1963. Prairie Nat. 10: 71-80.

A) 2; B) northcentral U.S.; C) Records of specimens and sightings.
Description - distribution.
Life History - dispersal.
Comments - A number of dramatic statistics are provided, e.g., in Cook County, Minnesota (NE corner), 147 lynx were bountied in 1962-63 and 137 more in 1963-64, although "not more than half a dozen" had been presented for bounty in that area in the previous 35 years; no more were reported until another (lesser) influx began, in 1971-72; increases in other areas are also reported (North and South Dakota, Montana, Manitoba, and Ontario) and some speculation on causes is offered; this is the best of the various reviews on the 1960's and 1970's "irruptions" in the continental U.S.

* Haglund, B. 1966. Winter habits of the lynx (*Lynx lynx* L.) and wolverine (*Gulo gulo* L.) as revealed by tracking in the snow. Viltrevy 4: 81-299.

A) 1; B) Sweden; C) Snow-tracking, winters of 1960-64.
Description - features.
Life History - food, activity, hmrange, movements, denning, behavior.
Population Dynamics - natality.
Comments - The larger European lynx (males to 24 kg, females to 22 kg) commonly prey upon roe deer and reindeer in winter, although hares and tetraonids are the primary prey on a year-round basis; daily movements averaged about 8 km; the home range of one male was estimated at about 300 km²; the animals are generally inactive during the day, and during bad weather.

** Halfpenny, J.C., S.J. Bissell, and D. Nead. 1979. Colorado wolverine-lynx verification program. Journal of Colorado-Wyoming Academy of Science 11(1):89.

This report presents the first results of a survey of historical, trapping, and sighting records of lynx in Colorado. The authors discuss the trend of the sighting reports which appears to be coincident with the 10-year lynx population cycle in Canada. During the late 1800's, 1960's, and 1970's Canadian lynx populations peaked. At the same time the number of trapped lynx and sightings of lynx increased. Similarly, during the low ends of the 1940's and 1950's cycles, there seems to be a decrease in trapping and sighting reports. The authors consider two hypotheses. The first is that during peaks of the Canadian lynx population cycles, lynx emigrate or disperse long distances. Second, the southern-most lynx populations may be synchronized with the northern populations in Canada.

* Iurgenson, P.B. 1955. Ecology of the lynx in forests of the central zone of the USSR. Zool. J. 34: 609-620.

A) 2; B) USSR; C) Regular snow-tracking, 1930's and 1940's.
Habitat Characteristics - vegetation, cover.
Life History - food, nutrition, hmrange, denning, behavior.
Population Dynamics - poptrend, harvest.
Habitat Management - forestry.
Comments - Estimated densities of one lynx per 7-20 km², depending on stage of cycle (i.e., only 3-fold differences between high and low); as in North America, hares were the primary food in most areas, and lynx numbers and movements were related to those of hares; in relation to peaks based on fur harvest records, the author notes that "...the yield is the result not of increase in the number of species which is being procured, but of a shortage of food."

* Keith, L.B. 1974. Some features of population dynamics in mammals. Proc. Internat. Congr. Biol. 11: 17-58.

A) 2; B) Mostly North America; C) Review of literature.
Life History - socbehav.
Population Dynamics - cycles, popreg.
Comments - This paper provides a useful summary of the various schools of thought on natural regulation of animal populations, then focuses on the following subjects: 1) impacts of predation on mammal populations, 2) predator population dynamics, 3) cyclic fluctuations, and 4) ungulate irruptions; in the context of this bibliography on lynx, the author summarizes 12 years of data on the snowshoe hare cycle at Rochester, Alberta, with the following conclusions: the cycle can be explained in terms of "...a hare-vegetation

interaction which initiates the (hare) population decline and sets the stage for a predator-hare interaction which extends it."; the population dynamics of lynx is compared to that of mountain lions--from available evidence it is concluded that unlike the case for mountain lions, lynx populations are not limited by social behavior (territoriality) because of their dependence on a fluctuating and unstable prey base (the cyclic hare).

* Keith, L.B., A.W. Todd, C.J. Brand, R.S. Adamcik, and D.H. Rusch. 1977. An analysis of predation during a cyclic fluctuation of snowshoe hares. Proc. Internat. Congr. Game Biol. 13: 151-175.

A) 2; B) Alberta; C) Synthesis of Rochester study results (hare, grouse, and predator populations) over one complete cycle.

Habitat Characteristics - study/area.

Life History - food.

Population Dynamics - poptrend, popreg, cycles.

Comments - This paper examines the response and role of several predators, including lynx, to changing snowshoe hare numbers; on average, predator populations showed a 4-fold change in numbers between peak and low (lynx = 3.8), while that for hares was 31.3; it is concluded that predator numbers and use of hares increases in response to increasing hare numbers, and may remain relatively high for 2-3 years following the hare decline--predator numbers eventually decline, but their continued pressure on the declining hare population may deepen and extend the hare low.

* Koehler, G.M. 1987a. Preliminary report: the ecology of the lynx in northcentral Washington. *In* B. Townsend (ed.). Abstracts of Pap. Pres., Fourth Northern Furbearer Conf., 3-4 April 1987, Alaska Dep. Fish and Game, Juneau.

A) 3; B) Washington; C) Mostly radio-tracking?

Description - distribution.

Life History - food.

Population Dynamics - natality, poptrend.

Comments - Abstract only: The study, an extension of one commenced in the area in 1980 (Brittell 1987), is to determine population dynamics and habitat requirements of a population occurring at the (southern) periphery of its range; preliminary findings are of low density (2.3-3.1 lynx/100 km^2) and low productivity (1-1.3 kittens/year), similar to parameters in more northerly populations during hare lows; foods in Washington include snowshoe hares, tree squirrels, and microtines.

* Koehler, G.M. 1987b. The ecology of the lynx (*Lynx canadensis*) in northcentral Washington. Unpubl. Prog. Rep., Wildl. Res. Inst., Univ. Idaho, Moscow. 25pp.

A) 3; B) Washington; C) Radio-tracking 7 animals (5 males, 2 females), and snow-tracking.
Descriptions - features, distribution.
Habitat Characteristics - study/area, vegetation, cover.
Life History - food, hmrange, socbehav, denning.
Population Dynamics - natality, mortality, poptrend.
Habitat Management - fire, forestry.
Comments - This is a report on a continuing study of lynx at the southern edge of their range, and just south of the B.C. border; a total of 28 different lynx have been handled on the study area since 1981; male home ranges averaged 67.8 km^2, while those of females were 41.5 km^2; the two radio-collared females produced 7 kittens in 1986 (July), but only 1 of those (14%) survived to winter--there was also an uncollared female with 3 kittens on the area in winter 1986-87; the two females also both had litters in July 1987, one apparently only having 1 kitten and the other undetermined; adult mortality is low, with annual rates among the collared sample of 21% from 1981-83, 27% for 1986, and 0% for 1987--one adult male is believed to have died as a result of predation (predator not specified); lynx selected for young lodgepole pine forests (both post-fire and post-logging) and mature spruce-subalpine fir forests--the pine types supported the most evidence of hare use, and thus were probably used primarily for hunting, while all 4 of the natal dens were found in mature conifer habitats with an abundance of blowdown; analysis of 33 scats indicated that the most used food was snowshoe hare (79.3% frequency of occurrence); other foods included red squirrels (24.1%), mule deer (6.9%) and deer mice (3.4%).

** Koehler, G.M. 1988. Demographic characteristics and habitat requirements of lynx (<u>Lynx</u> <u>canadensis</u>) in north central Washington. Unpublished Report. Idaho Cooperative Fish and Wildlife Unit. Universiyt of Idaho, Moscow.

This report illustrates a study in northcentral Washington, from 1985-1987, to determine population dynamics and habitat and prey requirements of lynx at the southern extension of their distribution.   Koehler monitored the density of lynx and productivity over the long term to determine whether lynx populations cycle at the southern edge of their distribution, as they do in the north.   Koehler mentions that more southerly snowshoe hare populations do not cycle as do populations in the north.

Methodologies discussed include ear and lip tattoos, trapping, radio telemetry and tranquilization. Researchers captured lynx in box-type live traps and #3 leg hold traps. Individuals were marked with eartags tattooed in the ear and lip and fitted with a radio collar.   Radio telemetry was used to determine habitat requirements, social organization, productivity and mortality. Movements were monitored by airplane at 7-15 day intervals and from the ground at 1-7 day intervals.   Home range size was determined

by the Minimum Convex Polygon Method. Females were monitored daily during spring and early summer to determine if they were denning or not. Cover types were determined by the USFS Geographic Information System. The proportion of forest types occurring within a home range was determined by digitizing.

Trapped lynx were anesthetized with 20 mg Ketamine Hydrochloride per kilogram of body weight, and weighed and measured to determine reproduction status. Age was determined by body size, condition of teeth, and whether the animal was accompanied by an adult female. The influence of prey distribution on lynx habitat use was determined by estimating the relative abundance of small mammals among forest types. This was accomplished by counting fecal pellets for hares and grouse, tree squirrels and their tracks were counted as well. Some management considerations are also provided.

Lynx were observed utilizing habitat types that are coincident with areas of higher snowshoe hare abundance. These areas were typified by the presence of lodgepole pines in an early successional fire-recovery state. However, lynx used more mature forests while denning. Mature forests were dominated by Engelmann spruce, Subalpine fir, and Lodgepole pine. Dens appeared to occur mostly on north and northeast aspects in areas exhibiting high concentrations of downfall.

Lynx diets as determined from this study consisted of 79% snowshoe hares and 24% tree squirrels. Koehler suggests that the scarcity of prey found in the southern limits of lynx distribution may account for the low density and low productivity of lynx in these areas.

ehler, G.M., M.G. Hornocker, and H.S. Hash. 1979. Lynx movements and habitat use in Montana. Can. Field-Nat. 93: 441-442.

A) 2; B) Montana; C) Radio-tracking, 2 adults, 1977.
Habitat Characteristics - study/area, cover.
Life History - hmrange, movements.
Population Dynamics - mortality.
Comments - An adult female, caught in mid-January, was monitored for only 2 weeks before it died, apparently killed by a cougar; an adult male was monitored for 7.5 months, during which time it used a home range of 36 km^2; 90% of 29 locations were in a young (67-year-old) burn thickly stocked with lodgepole pine and supporting good populations of snowshoe hares.

✶ McCord, C.M., and J.E. Cardoza. 1982. Bobcat and lynx. Pages 728-766 *in* J.A. Chapman and G.A. Feldhamer (eds.). Wild mammals of North America. Biology, management, and economics. Johns Hopkins Univ. Press, Baltimore.

A) 2; B) Holarctic; C) Review of literature.

Description - features, taxonomy, distribution.

Habitat Characteristics - vegetation, climate.

Life History - lifehist.

Population Dynamics - natality, mortality.

Species Management - age/tech, field/tech, repro, economics, harvest, harv/strategy, transplants.

Habitat Management - fire, forestry, other/impacts.

Other Topics - bibliography, physiology, morphology, genetics.

Comments - The biology and management of both lynx and bobcat are reviewed together, and some aspects are compared, although the bulk of the review is devoted to the more frequently studied bobcat; it is noted that since northern lynx are now considered one circumpolar species, researchers in North America should keep abreast of findings in Eurasia; most findings are summarized from other papers in the present bibliography-- additional items of interest are as follows: PHYSIOLOGY AND MORPHOLOGY - the lynx has well-developed eyesight and hearing, but a relatively poor sense of smell; it is well-adapted to cold, deep-snow conditions. REPRODUCTION - in both species, the corpea lutea do not degenerate into corpora albicantia--rather they persist through subsequent ovulations, although the recent and older corpora can be distinguished by structural and/or color differences; lynxes are assumed to be induced ovulators, but there is some evidence that bobcats may ovulate spontaneously; females are capable of breeding in their first year, but males may not be. MORTALITY - little is known of pre-natal mortality i either species, but high kitten mortality has been recorded for both species, especially during periods of food scarcity. There is little direct information on adult mortality other than that caused by humans. PARASITES AND DISEASES - documentation of diseases in wild populations of both species are scarce--no epizootics or die-offs from heavy parasite infestations have been recorded. It is speculated that "...they may be less vulnerable to this type of mortality due to their solitary nature and their propensity to change denning and resting areas frequently." ECONOMIC STATUS - the primary role of lynx in the economy is in its fur value; due to the cyclic nature of lynx harvests, it is difficult to express that value in terms of averages for any particular area, but in North America i recent decades the number of pelts produced have been 1400-9000 in Alaska, 130-975 in the contiguous U.S., and 13 000 to 53 000 in Canada; unlike the case for bobcats, depredations are of little interest or concern in the management of lynx. MANAGEMENT - transplants have thus far been attempted only in Europe, and at least one of those efforts appears to have been successful (see Cop 1977); it is noted that log- term, intensive research of representative populations of both species is needed to enable better design and interpretation of monitoring programs and more effective management.

* McKay, D.I. 1985. Lynx in Manitoba: situation report. Unpubl. Rep., Wildl. Branch, Manitoba Nat. Resources, Winnipeg. 4pp.

A) 3; B) Manitoba; C) Statement of management rationale and strategy.
Population Dynamics - poptrend.
Species Management - economics, harvest, harv/strategy.
Comments - The lynx harvest in Manitoba has decreased since 1978-79, reaching a low of 596 pelts in 1983-84, and the trend over the past 40 years has been for decreases in harvest at the cyclic peaks; some major considerations in lynx management are high pelt value, the problem of accidental lynx catches in sets for other furbearers even with reduced or closed seasons, potential "bootlegging" of pelts across jurisdictional borders from closed to open areas, and reaction of anti-trapping organizations to non-action in relation to low and/or declining populations; it is recommended that a national system be developed, to establish open seasons in relation to the varying population trend across the country, that actions be taken within the fur industry to "enable a reduction of pelt value during critical periods...", and that wildlife agencies increase their monitoring activities.

McKay, R. 1991. Biological assessment and inventory plan for the North American lynx (Felis lynx canadensis) in the Uinta Mountains. Utah Dept. of Natl. Res., Salt Lake City. 65 pp.

This document includes a literature and an annotated bibliography as well as an assessment of the status of the lynx in Utah, and an inventory plan for the Uinta Mountains.

X Mech, L.D. 1973. Canadian lynx invasion of Minnesota. Biol. Conserv. 5: 151-152.

A) 2; B) Minnesota; C) Compilation of incidental observations.
Description - distribution.
Life History - dispersal.
Population Dynamics - poptrend.
Comments - Notes that an "irruption" of lynx in 1962-63 subsided within 2 years, then recurred in 1972; most animals had little or no tooth wear and appeared to be in good

physical condition; although two instances of females with young were recorded, ti was presumed that most of the increase of animals was due to dispersal from Canada.

✷ Mech, L.D. 1977. Record movement of a Canadian Lynx. J. Mammal. 58: 676-677.

A) 1; B) Minnesota-Ontario; C) Observation of a marked lynx.
Description - distribution.
Life History - movements, dispersal.
Comments - A female lynx, believed young when captured and collared in northeastern Minnesota (November 1974), was taken by a trapper in southeastern Ontario, 483 km distant (January 1977).

✷ Mech, L.D. 1980. Age, sex, reproduction, and spatial organization of lynxes colonizing northeastern Minnesota. J. Mammal. 61: 261-267.

A) 3; B) Minnesota; C) Radio-tracking and ear-tagging (incidental captures during a wolf study), and examination of carcasses, 1972-1978.
Life History - hmrange, socbehav, dispersal.
Population Dynamics - natality, mortality, poptrend, popcomp.
Species Management - harvest.
Comments - The study animals were characterized as emigrants from Ontario and Manitoba, during cyclic highs in those provinces (especially in 1972); despite the absence of a secure resident population and little evidence of local reproduction, 215 animals were harvested in Minnesota in 1972, and 691 in 1973, as compared to only 88 in 1974 and 0 in 1975; there was some evidence that males were more vulnerable to harvest than were females; home ranges of studied animals were larger than those documented in other areas (females 51-122 km^2). males 145-243 km^2).

✷ Nava, J. 1970. The reproductive biology of the Alaska lynx. Unpubl. M.Sc. Thesis, Univ. Alaska, Fairbanks. 141pp.

A) 2; B) Alaska; C) Examination of 1105 lynx carcasses, 1964-65.
Population Dynamics - natality.
Comments - Yearlings predominated in the harvest (60%), but kittens were under-represented; Alaskan lynx breed in late March or early April and give birth in June; data on reproductive parameters suggested that decreased reproduction rather than mortality of young is the primary factor in declining populations.

Nellis, C.H. 1971. The lynx in the northwest. Pages 24-28 *in* S.E. Jorgensen and L.D. Mech (eds.). Symposium on the native cats of North America. U.S. Bur. Sports Fish. and Wildl.,Fed/ Bldg., Fort Snelling, Twin Cities, Minnesota.

A) 1; B) Idaho, Montana, Oregon, Washington; C) Review of harvest and management status.
Description - distribution.
Population Dynamics - poptrend.
Species Management - harvest, harv/strategy.
Habitat Management - forestry.
Comments - Lynx were considered common (increasing) in Montana, rare to common (increasing) in Idaho and Washington, and very rare (decreasing) in Oregon; a 3-month trapping season was in effect in Washington, but there was no closed season and the animal was classified as a predator, or was unclassified, in the three other states; the only data on numbers is from harvests--it is not known if the animal is cyclic in the Northwest, but a dramatic increase in harvest in 1962-63 is speculated to have been caused by dispersal from Canada following hare declines in 1961-63; logging is portrayed as a potential benefit to lynx in producing young forests in which hares thrive, but it is noted that the beneficial effect could be reduced by some silvicultural practices that, by design or inadvertently, reduce the utility of cut areas to hares.

Nellis, C.H., and L.B. Keith. 1968. Hunting activities and success of lynxes in Alberta. J. Wildl. Manage. 32: 718-722.

A) 3; B) Alberta; C) Snow-tracking, 1964-64 through 1966-67.
Habitat Characteristics - climate.
Life History - food, activity, movements.
Species Management - field/tech.

Comments - Trailed lynx made kill, on average, every other night; About 70% of the utilized prey (weight) was snowshoe hare, 17% was carrion, and 11% Ruffed Grouse; hunting effort was greater, and success lower, in 1967 when prey populations were highest--that result was postulated to be due to poorer hunting conditions, as related to snow cover characteristics, in that year.

* Nellis, C.H., and S.P Wetmore. 1969. Long-range movement of lynx in Alberta. J. Mammal. 50: 640

> A) 2; B) Alberta; C) Observations of a marked study animal.
> *Life History* - movements, dispersal.
> *Comments* - An adult male, resident in the Rochester study area for about 3 years, lost a foot in a trapping incident and subsequently moved 164 km northwest in 163 days, and was shot in a chicken coop; both lynx and hare populations in the study area were increasing at the time.

* Nellis, C.H., S.P. Wetmore, and L.B. Keith. 1972. Lynx-prey interactions in central Alberta. J. Wildl. Manage. 36: 320-329.

> A) 3; B) Alberta; C) Snow-tracking, opportunistic study of marked animals, scat analysis, and autopsy of carcasses from trappers,1964-1967 (period of low and beginning of increase phase for hares).
> *Life History* - food, nutrition, hmrange, movements.
> *Population Dynamics* - natality, mortality, poptrend, popreg, cycles.
> *Species Management* - repro.
> *Comments* - The winter diet of lynx on the Rochester study area consisted of 76% hare, 10% carrion, 9% Ruffed Grouse, 3% red squirrel, and 2% small mammals and birds; average home range size for adults was estimated at 15 km²; the estimated study area lynx population during the 1964-65 through 1967-68 winters, respectively, was 11, 5, 3, and 9, with kittens present (6) only in the last year;the only documented adult mortality was at the hands of humans (3-4 of 17), although the fates of the others was not known;there was some evidence that mortality occurs primarily in winter,and was highest in the unusually severe winter of 1964-65; low to nil recruitment during the low of the hare cycle was believed due primarily to early kitten mortality rather than reproductive failure.

* O'Connor, R.M. 1984. Population trends, age structure, and reproductive characteristics of female lynx in Alaska, 1961 through 1973. Unpubl. M.Sc. Thesis, Univ. Alaska, Fairbanks. 111pp.

> A) 3; B) Alaska; C) Examination of 3130 carcasses collected over one complete population cycle, 1961-62 through 1972-73.
> *Life History* - dispersal.
> *Population Dynamics* - natality, poptrends, cycles.
>
> *Species Management* - age/tech, kill/tech, repro, economics, harvest, harv/strategy.
> *Comments* - A major factor in forcing increased recent interest in lynx management in Alaska has been fur value, with average pelt price increasing 8-fold ($35 to $263) between 1970-71 and 1982-83; CITES (Convention on International Trade of Endangered Species) is also described as a catalyst to recent research, in its requirements that signatory

✶ Parker, G.R. 1981. Winter habitat use and hunting activities of lynx (*Lynx canadensis*) on Cape Breton Island, Nova Scotia. Pages 221-248 *in* J.A. Chapman and D. Pursley (eds.). Worldwide Furbearer Conference Proceedings, Aug. 3-11, 1980, Frostburg, Maryland.

A) 3; B) Nova Scotia; C) Snow-tracking, 192 km of lynx trails, January through mid-April 1978.

Habitat Characteristics - study/area, vegetation. cover, climate.

Life History - food, nutrition, activity, movements, denning, behavior.

Species Management - field/tech.

Comments - Lynx were selective in use of habitat types, apparently preferring mature conifer and advanced successional (22-28 years post-logging) types; 198 of 200 hunting chases were directed at snowshoe hares, and overall success rate was 17%; hunting success improved through the winter (14% in January to 26% in April), and may have been due to changing snow conditions and/or increased experience of young lynx; individuals traveled an average of about 8 km and killed an average of one hare per day (24 hours); hunting success increased with group size, as animals hunted in a fanned-out, cooperative fashion.

✶ Parker, G.R., J.W. Maxwell, L.D. Morton, and G.E.J. Smith. 1983. the ecology of the lynx (*Lynx canadensis*) on Cape Breton Island. Can. J. Zool. 61: 770-786.

A) 3; B) Nova Scotia; C) Radio-tracking, snow-tracking, necropsy of carcasses from trappers, analysis of harvest data.

Description - features, distribution.

Habitat Characteristics - study/area, vegetation, cover.

Life History - food, nutrition, activity, hmrange, movements,health, behavior.

Population Dynamics - natality, mortality, poptrend, popcomp.

Species Management - age/tech, field/tech, repro, harvest, interactions, harv/strategy, refuges.

Habitat Management - forestry, other/impacts, hab/strategy.

Comments - This study involves a lynx population that is completely isolated from the continental population; the sex ratio of harvested animals was high to males in 1977-78 (68:32), but did not differ from 1:1 in the following 2 years; yearlings comprised the dominant age class in the harvest (52%, 67%, and 39%), while kittens declined (29% to 9% to 2%) during the 3 years of study; within the trapping season, the proportion of yearlings decreased from November through March, while kittens increased and the proportion of adults remained fairly stable during that period--females were more abundant in the harvest in November and December,with males dominating later; the proportion of parous females (those with placental scars) decreased progressively over the 3 years, but particularly in the case of yearlings (67%, 29%, 0%)--numbers of placental scars also decreased in yearlings (3.7, 2.7, -), but increased in older females (3.3, 3.8, 3.8); the above patterns coincided with a decline of snowshoe hares (1000/100 ha in 1977 to 170/100 ha in

jurisdictions justify their management programs; this study appears to be the first based on carcasses collected over one complete cycle, and involves the largest collection of lynx specimen material analyzed in any one study; questionnaire results on relative abundance of hares and lynx during the study period were considered more reliable indicators of population trends than were harvest records; regional differences (asynchrony) in the lynx cycle was documented, but it was noted that implementation of management at the regional level may be premature, because the importance of lynx dispersal in local population processes is yet to be evaluated; lynx populations fluctuated in response to hare abundance, becoming abundant, peaking, or becoming scarce 1 year after hares reached similar levels in 8 of 9 region-winters--however, harvest did not peak at the same time as the population, but followed the peak by up to 3 years; significant differences in age structure of the harvest sample occurred between regions in 6 of 10 winters and between some winters in all regions; approximately 3/4 of the harvest was composed of young animals (kittens plus yearlings) during first winters following hare abundance, but that reversed to 3/4 adults during first winters following years of hare scarcity; the highest proportion of kittens occurred from 1 to 4 winters prior to lynx populations, nor afterward as reported elsewhere; all measures of lynx reproduction, for both yearlings and adults, were higher when hares were abundant than when hares were scarce; yearlings were less productive than adults, but that was particularly evident during periods of hare scarcity; between periods of hare abundance and scarcity, yearlings decreased in ovulation rate from 97% to 18% and in implantation rate (among ovulators) from 72% to 18%l judging from the correlation between measures of lynx productivity and hare abundance, nutrition is probably the primary cause of observed differences during the cycle; lynx population levels could not be reliably predicted solely from data on reproductive rates from the previous year, probably because other factors such as neonate mortality and dispersal are occasionally more important; this study indicates that the temporal and regional relationships among lynx recruitment, lynx population peaks, and lynx harvest peaks may not be as simple as previously thought--it is noted that "...declines are detected *after* they occur by examining records of harvest...(and)...at that point lynx reproduction may already have declined for several years and it may be relatively late for an effective response by the manager."

* O'Connor, R.M., D. J. Reed, and R.O. Stephenson. 1987. Lynx population dynamics and harvest-insight from a computer model. *In* B. Townsend (ed.). Abstracts of Pap. Pres., Fourth Northern Furbearer Conference, 3-4 April 1987, Alaska Dep. Fish and Game, Juneau.

A) 3; B) general; C) Modeling of lynx population dynamics from data presented in the literature.

Population Dynamics - natality, poptrends, popcomp.

Species Management - harvest, harv/strategy.

Comments - Abstract only: The population dynamics model was designed to "...Maximize the interpretive value of our harvest data..."; preliminary conclusions are that 1) lynx populations have a large potential for increase under favorable conditions, 2) small changes in sex ratio may substantially affect population growth during hare abundance, and 3) "In some situations, a...population harvested at two different rates may yield the same three-year harvest; however, the number of lynx remaining after the three-year harvest may be much higher with the lower harvest rate."

1979 in the best habitats); fat deposits were least in yearling lynx--incidence and extent of fat on harvested animals declined from November through December, but increased or leveled off from January through February; by far the primary dietary item was snowshoe hare (97% occurrence in winter stomachs, 93% in winter scats, and 70% in summer scats)--white-tailed deer was second (5%, 5%, and 9%, respectively), while small mammals (especially red-backed vole and red squirrel) and unidentified birds accounted for most of the remainder; daily/seasonal activity, movements, and home range patterns for 3 radio-collared animals (1979) are described--seasonal home ranges of the two adults (male: 12 and 26 km^2; female 19 and 32 km^2) overlapped considerably, with the female's range approximately 30% larger than that of the male in both winter and summer; for both adults, summer home ranges were almost twice as large as those in winter; the juvenile, a female, had a smaller and less seasonally variable home range (10 and 8 km^2), maintained separate from those of the two adults; hunting success of lynx increased as winter progressed, and was greater for groups (usually females with young) than for single animals; a density of 20 lynx/100 km^2 was estimated for the 60 km^2 study area in winter 1978-79; 65% of the projected population was removed by trapping in the following winter--there is evidence that vulnerability to trapping is related to body condition and/or experience, thus explaining the harvest pattern of yearlings and/or leanest animals early in the winter and other, more experienced or protected (kittens with their mothers) classes later; because there is little "refuge" area on Cape Breton Island, the recommended harvest management strategy is for restricted harvests (e.G., by trapper quotas) in years of high recruitment and closures during the lows--monitoring of snowshoe hare densities and of sex and age structure of the harvest are believed essential for effective regulations; it is also noted that there is potential for reducing overall harvests and changing harvest composition by manipulating timing and duration of the trapping season; extensive clearcutting of the mature conifer forest on the island is considered a potential threat to the island lynx population; collared animals selected for regenerating mixed forest habitats--the best local habitats for snowshoe hares--but large clearcuts are of little use to either hares or lynx in winter for the first 20 years, and may be used only at the periphery for many years thereafter; it is considered too late to integrate forest and lynx (hare) management on the island, but it is implied that reduction of clearcut size and interspersion of uneven-aged cuts and mature forest would have been desirable; there is some evidence that the bobcat, recently arrived on the island, may be competitively excluding lynx in the lowlands.

Quinn, N.W.S., and J.F. Gardner. 1984. Relationships of age and sex to lynx pelt characteristics. J. Wildl. Manage. 48: 953-956.

A) 3; B) Ontario; C) Study of trapped specimens, 1979-1982.
Description - features. .
Species Management - age/tech, kill/tech, harv/strategy.
Comments - Kits of both sexes can be reliably separated from other classes of lynx by pelt measurements, thus giving managers a method for monitoring recruitment at the fur-sale level; separation of other classes by pelt measurements is less clear although extra-large pelts are almost always from males.

✗ Quinn, N.W.S., and G. Parker. In Press. Lynx. Chapter *in* M. Novak, J.A. Baker, M.E. Obbard, and B. Malloch (eds.). Wild furbearer management and conservation in North America. Ontario Trappers Assoc., North Bay.

A) 2; B) North America; C) Review of literature.
Description - features, taxonomy, distribution.

Habitat Characteristics - vegetation.
Life History - lifehist.
Population Dynamics - cycles, natality, mortality, popcomp, poptrend.
Species Management - age/tech, field/tech, economics, harv/strategy, transplants.
Habitat Management - hab/strategy.
Comments - This paper summarizes lynx biology and management based on the authors' management and research experience in eastern Canada, and are all listed elsewhere in the present bibliography. From the many topics covered some of the major points relating to management are as follows: In conifer-dominated habitats, dense softwoods with shrub openings of 2-4 ha are considered ideal for hares, and therefore for lynx hunting habitat; it is suggested that because lynx are relatively docile in traps, trappers can practice selectivity by releasing nontarget animals, e.g., adult females--some verbal instructions are given; it is noted that identifying kittens in fur samples may be the easiest way of monitoring population recruitment, but may not be the most reliable if trapping biases are not taken into account; factors managers should be aware of in setting seasons include "...differential vulnerabilities to trapping throughout the season, and the relationship of age, sex, and period of capture to pelt value."; the "minimum data set" for managing lynx populations include chronology of harvest statistics and hare abundance, carcass analyses in relation to harvest and hare data, annual lynx abundance indices, and keeping abreast of relevant literature; wildlife and forest practices producing small strip or block cuts are beneficial to hares and lynx, while extensive clearcutting "is unacceptable"; lynx were successfully introduced into southeastern Ontario in the 1950's (no details given).

✳ Quinn, N.W.S., and J.E. Thompson. 1985. Age and sex of trapped lynx, *Felis canadensis*, related to period of capture and trapping technique. Can. Field-Nat. 99: 267-269.

A) 3; B) Ontario; C) Analysis of carcasses and harvest data, 1979-1982.
Life History - activity, behavior.
Population Dynamics - popcomp.
Species Management - age/tech, harvest, harv/strategy.
Comments - Age and sex composition of the harvest changed within the trapping season, with yearlings comprising a high proportion of the early harvest, kits increasing in January and February, and adults remaining a fairly constant proportion throughout; it is believed that males are more vulnerable to leg-hold trap sets that are females; the Ontario population was "rapidly increasing" at the time of the study, and it is acknowledged that the composition of the harvest at other phases of the cycle would differ from that observed.

Quinn, N.W.S., and J.E. Thompson. 1987. Dynamics of an exploited Canada lynx population in Ontario. J. Wildl. Manage. 51: 297-305.

A) 3; B) Ontario; C) Analysis of harvest data and 993 carcasses, 1979-1982.
Habitat Characteristics - study/area, vegetation.
Population Dynamics - natality, mortality, poptrend, popcomp.
Species Management - age/tech, kill/tech, repro, economics, harvest, harv/strategy.
Comments - Composition, estimated annual mortality, productivity, and physical condition of trapped lynx were compared in tow broad habitats (Boreal Mixed Wood and True Boreal Forest), and in three areas of differing harvest density (0.34, 0.70, and 1.71 lynx/100 km^{2}0; both hare and lynx populations were increasing during the study period; studied parameters varied little across the comparison areas; the 3-year harvest was characterized by an abundance of yearlings and was significantly dominated by males; it is concluded that males, especially the yearlings, are the most vulnerable to trapping; productivity was high, with almost all yearling and adult females and one-third of kittens having bred, and with average apparent litter size (placental scar counts) of 4.18; average annual mortality rates of 46% for males, 28% for females, and 38% overall were estimated, and it was noted that the population nevertheless increased at those rates.

Saunders, J.K., Jr. 1963a. Food habits of the lynx in Newfoundland. J. Wildl. Manage. 27: 384-390.

A) 2; B) Newfoundland; C) Analysis of 206 digestive tracts and 220 scats, 1956-1961.

Life History - food, nutrition, behavior.
Comments - Snowshoe hare was the most used food throughout the year (73% occurrence), with highest use in winter and spring; other foods, especially microtines and birds, were most frequent in spring and summer, though still less than hares; carrion, mostly moose remains from the fall hunting season, was commonly used in winter; food requirements, and kills, amounted to the equivalent of about one hare every 2 days.

Saunders, J.K., Jr. 1963b. Movements and activities of the lynx in Newfoundland. J. Wildl. Manage. 27: 390-400.

A) 2; B) Newfoundland; C) Snow-tracking and live-trapping, 1956-1961.
Life History - activity, hmrange, movements, behavior.
Species Management - field/tech.
Comments - Most recaptures of tagged animals were within a few km of original capture sites although one animal, a male, dispersed 103 km after being resident for several months;three animals that travelled together in one winter proved to be an adult female with her two female kittens; daily movements ("cruising distances") averaged about 8 km, and the home ranges of the female with kittens and two males were, respectively, 15.5, 18.1, and 20.7 km^2; most activity occurred at night, but at a decreased level during storms.

* Saunders, J.K., Jr. 1964. Physical characteristics of the Newfoundland lynx. J. Mammal. 45: 36-45.

A) 2; B) Newfoundland; C) Examination of trapped specimens.
Description - features.
Life History - pelage.
Species Management - age/tech.
Comments - Among animals over 1 year old, males were generally larger than females, but there were overlaps--mean weight for 93 males was 10.7 kg (range 6.4-17.2) and for 91 females was 8.6 kg (5.0-11.8); moult to winter pelage occurred by October and moult to summer pelage was in progress by April; some measurements on newborn and other very young animals are given; kittens may be distinguished by small body size and by deciduous or erupting permanent teeth; yearling females are almost as large as adult females; and have fully adult dentition by the end of their second year; yearling males are smaller than adult males, with only small sagittal crests and with the permanent lower canines not fully developed.

* Slough, B.G. 1986. Lynx status and management in the Yukon. Interim Rep., Yukon Dep. Renewable Resources, Whitehorse. 15pp.

A) 3; B) Yukon Territory; C) Literature review plus assembly of harvest and questionnaire data.
Population Dynamics - poptrend, popcomp.
Species Management - census, harvest, harv/strategy.
Comments - The most recent hare population crash was well-documented, with numbers dropping to 6% of peak densities within 2 years; trapping pressure is believed to have dropped in response to subsequent reduced lynx abundance, but there are concerns it may still be too high as a result of high fur prices; kittens comprised about 7% of the harvest in the fourth year after the hare decline, but with differences between areas (almost twice as many from Dawson as from Whitehorse); untrapped refugia are believed important during the cyclic low, and the only management change in recent years has been a shortening of the season from 5 to 4 months, eliminating March; a complete season closure during the low is recommended as "...the most biologically and economically sound management strategy over the long term."

* Stephenson, R.O. 1986. Development of lynx population estimation techniques. Alaska Dep. Fish and Game, Unpubl. Pittman-Robertson Prog. Rep., W-22-2,3,4, job 7.12R, Juneau. 84pp.

A) 3; B) Alaska; C) Radio-tracking, aerial and ground transects, scat analysis, necropsy of carcasses, interviews, analysis of harvest data.
Habitat Characteristics - vegetation.
Life History - food, activity, hmrange, socbehav, movements, dispersal, health, denning, behavior.

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Population Dynamics - natality, mortality, poptrend, popcomp, cycles.

Species Management - census, age/tech, repro, harvest, harv/strategy.

Comments - The studies were undertaken during the decline and low phase of the hare cycle; one male and two female lynx spent a combined total of about 65% of their time inactivity and 35% resting; home ranges for 5 of 6 animals were fairly stable, averaging 77 to 121 km² (based on 95% and 100% of locations, respectively); some shifts in home range over time were noted; one animal, a female, dispersed a minimum of 169 km from a range used for at least 2 months prior to the dispersal; lynx used a variety of habitats, perhaps mostly in relation to availability, although large openings were avoided; mating activity peaked during about the third week of March; there is evidence that the hare and lynx peaks in the early 1980's were considerably lower than the previous three peaks, and populations in the mid-1980's were very low; estimated densities in various sections of the study area were comparable to those obtained during the cyclic low in other areas, ranging from 1 lynx/17.4 km² to 1 lynx/69.4 km²; the author feels that aerial and/or ground transects to record lynx tracks in snow have good potential for providing indices of lynx abundance, and explicit descriptions and instructions are provided; kittens were rare in Alaskan fur harvests between 1982 and 1985, coinciding with the local hare low as in other areas; none of 40 animals were over 4 years old, possibly reflecting previous poor production and/or heavy trapping pressure; a large proportion of the animals caught by trappers during the study, almost 50%, were judged to have been in less than good condition; analysis of reproductive tracts "...revealed a low rate of ovulation and breeding compared with rates during periods of hare abundance"; snowshoe hares were the most used food items, occurring in 70% or more of study samples, while microtine rodents, birds and red squirrels were also used commonly; several instances of predation (on red foxes, caribou and Dall's sheep) are documented.

* Todd, A.W. 1985. The Canada lynx: ecology and management. Canadian Trapper 13(2): 15-20.

A) 3; B) Canada, mostly Alberta; C) Summary of current knowledge for the layman.

Life History - lifehist.

Population Dynamics - poptrend, popcomp, cycles.

Species Management - economics, harvest, harv/strategy.

Other Topics - history.

Comments - This is not a report of original research, but is a good, thoughtful summary of the lynx management problem, with emphasis on the Alberta situation; the effect of high pelt prices in increasing and intensifying trapping pressure is emphasized--it is noted that although average prices have been very high in the 1980's, top prices of more that $1000 better illustrate the incentive value of trapping for lynx even when they are scarce; most illustrations of population trends are based on harvest records, with additional reference to results of the Rochester studies for recent decades in Alberta; it is believed that declines in lynx harvest in the early decades of this century were due to overexploitation at around the turn of the century, and that continued low harvests in the 1940's and 1950's were due at least in part to very low prices and demand; the great harvest increases in the 1960's and

1970's cycles are attributed to recovered populations and increased prices, while the decline in the 1980's is thought due primarily to overexploitation as a result of greatly increased interest in lynx trapping during the previous decades--alternate explanations that might explain part of the recent harvest decline include permanent (agriculture) and temporary (fire, logging, succession) habitat losses, industrial development impacts, effects of a severe winter (1981-82) on the animals and/or on trappers, and smaller hare population levels; the author makes a case for "progressive management" involving, at least, shortened or closed seasons during years of declining and low populations, and compulsory inspection and registration of pelts.

✶ Tumlison, R. 1987. *Felis lynx*. Mammalian Species No. 269, Amer. Soc. Mammalogists. 8pp.

> A) 2; B) Holarctic; C) Review of existing literature.
> *Description* - features, taxonomy, distribution.
> *Habitat Characteristics* - vegetation.
> *Life History* - lifehist.
> *Population Dynamics* - natality, mortality, poptrend, popreg, cycles.
> *Species Management* - age tech. economics, harvest, harv/strategy.
> *Habitat Management* - hab/strategy.
> *Other Topics* - bibliography, paleontology, zoogeography, physiology, genetics.
> *Comments* - Management-related information is as reviewed from other papers in the present bibliography.

✶ Van Zyll de Jong, C.G. 1966a. Food habits of the lynx in Alberta and the Mackenzie District, N.W.T. Can. Field-Nat. 80: 18-23.

A) 2; B) Alberta and NWT; C) Analysis of 75 digestive tracts (52 winter and 23 summer).
Life History - food.
Comments - In terms of frequency of occurrence, snowshoe hare was the most common item in winter (72%) and in summer (52%); microtines were important in both seasons, at 10% in winter (all *Microtus*) and 31% in summer (22% *Microtus* and 9% *Clethrionomys*); other mammals eaten included red squirrel, two species of ground squirrel, beaver, and deer; birds occurred in 23% of winter tracts (10% grouse and 13% unidentified) and in 35% of summer samples (4% grouse, 4% Gray Partridge, 9% duck, and 17% unident.); the lynx population was believed high and the snowshoe hare still relatively high, but declining, when the samples were obtained.

* Van Zyll de Jong, C.G. 1966b. Parasites of the Canada lynx, *Felix (Lynx) canadensis* (kerr). Can. J. Zool. 44: 499-509.

A) 1; B) Alberta, NWT; C) Necropsies of 113 carcasses and examination of 15 live animals.
Life History - health.
Comments - The specimen collection was made in 1961-1963, during a "high" in the lynx population; parasites in the small intestine included 4-5 species of cestodes (mostly *Taenia*), 1 trematode, and 2 species of nematodes, at infection rates ranging from 1 (the trematode *Alaria*) to 85% (*Taenia laticollis*); all other endoparasites were nematodes, 2 species from the stomach and 1 in the lungs; only 3 of 113 animals had no endoparasites; no ectoparasites were found on 18 animals examined, but a flea normally found on red squirrel was provided separately from a hunter-shot lynx; there was no indication that any of the lynx examined were adversely affected by their parasite loads.

* Van Zyll de Jong, C.G. 1971. The status and management of the Canada lynx in Canada. Pages 16-22 *in* S.E. Jorgensen and L.D. Mech (eds.). Symposium on the native cats of North America. U.S. Bur. Sports Fish. and Wildl., Fed. Bldg., Fort Snelling, Twin Cities, Minnesota.

A) 2; B) Canada; C) Review of information from provincial and territorial sources.
Description - distribution.
Population Dynamics - poptrend.
Species Management - harvest.
Other Topics - history.
Comments - It is noted that the species' range expands temporarily during years of abundance, but that its true range should be considered as that area supporting animals both during the highs and lows of the cycle; the species still occurs over most of its pristine range in Canada, although it is rare or absent in heavily developed areas to the south, and it is essentially extinct in New Brunswick, Prince Edward Island, and possibly mainland Nova Scotia; bases on historic fur records, it is noted that production during peak years between 1820 and 1919 ranged from 30 000 to 80 000 pelts, but that declines occurred there after, especially in the 1940's and 1950's when, ti is said, "...populations failed to peak in most parts of Canada."--both over trapping and habitat changes have been implicated; at date of writing, lynx were managed as fur animals, with closures during seasons when pelts are not prime, in all jurisdictions except Newfoundland (no closed season; control as predator in some caribou calving areas); it is noted that in the larger provinces "...trapping is largely on registered traplines which tends to reduce trapping pressure: and there was additional management in Ontario in the form of quotas; the potential for over-harvest during the cyclic low is discussed, citing evidence from "...southern, more intensively trapped registered traplines and unorganized trapping areas" which now apparently depend mostly on immigration from other areas; it is suggested that should more intensive management be required in the future, it should be "...geared to the different phases of the cycle" (and) "...protection during (population) troughs should be considered in at least some areas."

✴ Ward, R.M.P. 1985. Behavioral responses of lynx to declining snowshoe hare abundance. Unpubl. M.Sc. Thesis, Univ. of B.C., Vancouver. 106pp.

A) 3; B) Yukon; C) Radio-tracking (6 males, 5 females) over a 2+ year period, plus snow-tracking.
Life History - food, hmrange, socbehav, movements, dispersal,health.
Population Dynamics - mortality, poptrend, cycles, popreg.
Species Management - harvest, harv/strategy.
Comments - Lynx biology described in relation to snowshoe hare abundance (decline phase only); see Ward and Krebs (1985), below; the author notes that although study results to date are suggestive, showing high rates of trapping mortality among study animals and indicating particular vulnerability to trapping during the low in the hare cycle, there are still some important inconsistencies and data gaps.

✱ Ward, R.M.P. 1987. The lynx harvest: are refugia maintaining lynx populations? *In* B. Townsend (ed.). Abstracts of Pap. Pres., Fourth Northern Furbearer Conference, 3-4 April 1987, Alaska Dep. Fish and Game, Juneau.

A) 3; B) General; C) Computer modelling of population dynamics data from the literature.
Population Dynamics - poptrend, cycles.
Species Management - harvest, harv/strategy.
Comments - Abstract only: The model developed supports concerns expressed by wildlife managers in relation to the potential for overexploitation of lynx populations during the cyclic low; simulated lynx populations went to extinction at sustained harvest rates of more than 34% for 10 years, but with closures during 3 years of the low, a harvest rate of 41% could be applied for the remaining 7 years of the cycle; it is noted, however, that human-related mortalities based on radio-collared samples (81% of all studies combined) is higher than recruitment during any stage of the cycle, thus suggesting that "...refugia from trapping may be maintaining and stabilizing lynx over large geographic areas."

✱ Ward, R.M.P., and C.J. Krebs. 1985. Behavioural responses of lynx to declining snowshoe hare abundance. Can. J. Zool. 63: 2817-2824.

A) 3; B) Yukon; C) Radio-tracking plus snow-tracking transects (see Ward 1985, above).
Life History - food, hmrange, socbehav, movements, dispersal, health.
Population Dynamics - mortality, poptrend, cycles.
Species Managements - harvest, harv/strategy.

Comments - This is the published elaboration of the biology section in Ward (1985); following the crash of the Hare population, lynx home ranges increased 3-fold, from 13.2 to 39.2 km²; home ranges did not differ significantly in size between the sexes, and

overlapped considerably between and among sexes; at prey densities below about 0.5 hares/ha, some lynx (3 females) appeared to "...abandon their home ranges and become nomadic."; 3 of 7 collared animals dispersed more than 250 km, up to 700 km, during the rapid decline phase of the hare cycle in 1982--those movements were during the May-October (snowfree) period; no such dispersals were recorded among 4 newly collared animals the following year, when hare densities, though low, had stabilized; daily movements of collared lynx were 2.2-2.7 km/day at hare densities above 1.0 hare/ha, but increased to 5.5 km /day at densities below that; it is concluded that the observed increased activities, range sizes, and dispersal were behavioral responses to the hare decline, to enable individuals to meet their energetic requirements; only 3 of the 11 collared animals survived for more than 1 year--the 8 losses included 7 animals taken by trappers outside the study area and 1, a female, that is believed to have starved in winter 1983-84; only 1 of 9 animals that left the study area, where human harvest is prohibited, is believed to have survived; it is noted that lynx are probably most vulnerable to trapping during the hare decline, when they are both hungry (thus more likely to be attracted to baits) and mobile (thus more likely to contact traps), and that they are probably therefore particularly sensitive to overharvesting at such times.

✶ Ward, R.M.P., and B.G. Slough. 1987. Lynx management progress report, 1986/87. Pages 33-56 *in* B.G. Slough, and R.M.P. Ward. Annual Prog. Rep., Furbearer Manage. Program, Yukon Dep. Renewable Resources, Whitehorse.

A) 3; B) Yukon; C) Analysis of harvest data; telemetry.

Habitat Characteristics - study area.

Population Dynamics - natality, poptrend, popcomp.

Species Management - census, field/tech, harvest.

Comments - Harvest declined 24% from the previous year, but populations of both lynx and hares were considered at least stable; based on pelt measurements, the proportion of kittens increased slightly, to 9.3% overall, with the Dawson sample still showing twice the kitten proportion as that from the Whitehorse area; telemetry data indicate that "refugia...are producing a surplus of lynx for the 'traplines'"; telemetry studies have begun in the Teslin burn area to assess the role of refugia, determine the nature of trapping mortality in relation to natural mortality, monitor lynx recruitment in relation to hare abundance, and develop techniques for monitoring lynx populations; a total of 6 lynx (4 males, 2 females) have been radio-collared, and all but one of the males has remained in the study area; both females produced litters--3 and 4 kittens, all of which were ear-tagged; population density will be assessed by a track transect method.

Wing, L.W. 1953b. Cycles of lynx abundance. J. Cycle Res. 2: 28-51.

A) 1; B) Northern Canada; C): Consideration of historic lynx fur returns.
Population Dynamics - cycles.
Comments - A detailed account of the nature of mathematical cycles, and discussion of the lynx harvest cycles in that context; an average cycle length of 9.6 years calculated for the lynx data.

Winterhalder, B.P. 1980. Canadian fur bearer cycles and Cree-Ojibwa hunting and trapping practices. Am. Nat. 115: 870-879.

A) 1; B) Canada; C) Review of historical and anthropological literature.
Population Dynamics - cycles.
Species Management - harvest.
Comments - Acknowledging that recent biological studies have confirmed the existence of the hare-lynx cycle, the author nevertheless questions the accuracy of early lynx fur return data in defining and quantifying historic trends; evidence is presented showing that during hare lows, native trappers were often forced into devoting most of their energies into food gathering, and often ceased or greatly reduced hunting for fur at those times.

Copies of the following literature on lynx appear here in their entirety (except for Brittell et al. 1989):

Brand and Keith 1979

Brand et al. 1976

Brittell et al. 1989

Carbyn and Patriquin 1983

Destefano 1987

Eisenberg 1982

Fox 1978

Hash 1990

Jackson 1961

Koehler 1990

Koehler 1990

Koehler and Brittell 1990

Koehler et al. 1979

McCord and Cordoza 1982

Parker et al. 1983

Quinn and Parker 1987

Quinn and Thompson 1987

LYNX DEMOGRAPHY DURING A SNOWSHOE HARE DECLINE IN ALBERTA

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Abstract: Demographic changes in lynx (*Lynx canadensis*) populations in Alberta were studied by examining 1,108 lynx carcasses collected from trappers during winters 1971–72 through 1975–76. Both snowshoe hare (*Lepus americanus*) and lynx populations declined during this interval from their cyclic peaks to low levels. Indices of consumption rates by lynx decreased with declining hare population levels. Concomitant decreases in indices of body fat of lynx during late winter suggested that lynx experienced a negative energy balance during hare scarcity. Lynx pregnancy rates and litter sizes also decreased during the population decline. Annual finite rates of reproductive increase fell 38%. Kittens were underrepresented in trapped samples; the proportion of kittens in adjusted age ratios dropped from 66% during 1971–72 (year of hare abundance) to 3% during 1973–76 (years of hare scarcity). Postpartum mortality of kittens, ranging from 65 to 95%, was the predominant cause of lowered recruitment to winter populations. Rates of trapping mortality were positively related to average pelt value, and appeared additive to nontrapping mortality. By curtailing lynx trapping during 3 years of population decline, we estimated that the total Alberta lynx harvest during 5 years of subsequent increase would be greater than that of a continuously trapped population. We suggest curtailment of lynx trapping for 3–4 years starting with the 2nd year after the peak in fur harvests.

Recent increases in raw fur prices have increased the possibility of overexploiting lynx populations in North America. The average price of lynx pelts in Canada, for example, rose from \$38 to \$216 between 1971–72 and 1975–76 (Statistics Canada 1973, 1977). In Alaska, improved access to remote areas from road construction during oil and mineral exploration and development, along with the advent of snowmobiles and all-terrain vehicles, have greatly enhanced the mobility and efficiency of trappers (Berrie 1974:39). Similar events have occurred in Canada. Long-term studies of lynx population dynamics are needed to provide a basis for responsible management decisions.

Snowshoe hares are the staple food of lynx at all phases of the 10-year cycle (Saunders 1963*b*, van Zyll de Jong 1966, Nellis et al. 1972, Brand et al. 1976). This

reliance of lynx upon hares explains the correspondence between lynx and hare cycles (Elton and Nicholson 1942, Keith 1963). Brand et al. (1976) summarized both the dietary and numerical responses of lynx to changing hare densities near Rochester, Alberta, during the winters of 1964–65 through 1967–68 and 1971–72 through 1974–75. In conjunction with these investigations of lynx populations at Rochester, we collected lynx carcasses from trappers throughout forested regions of Alberta during the winters of 1971–72 through 1975–76. Our objective was to increase understanding of demographic mechanisms of region-wide lynx populations. In this paper we examine changes in diet, physical condition, reproductive performance, sex and age structure, and mortality of regional lynx populations in relation to changes in hare abundance.

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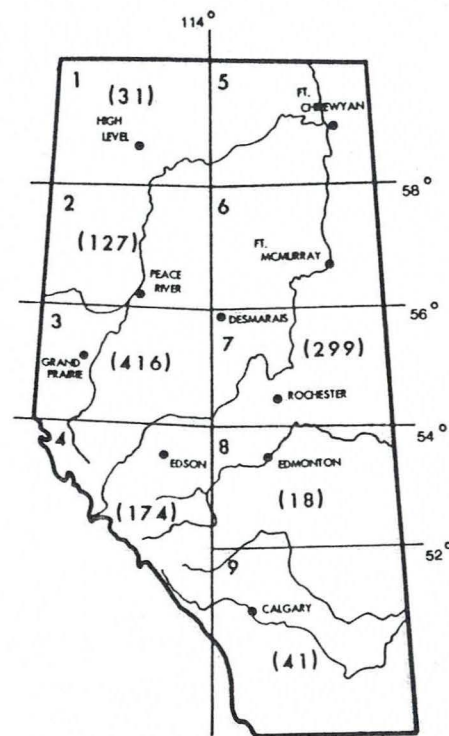
Fig. 1.   Number of lynx carcasses (in parentheses) collected from trappers in 7 regions of Alberta during the winters of 1971–72 through 1975–76.

Services Branch); The Research Council of Alberta; and the National Science Foundation (Grant No. GB 33320X).

MATERIALS AND METHODS

Snowshoe Hare Population Trends.—Population indices were calculated for Alberta from questionnaires sent to approximately 600 registered trappers each January from 1963 through 1976. Trappers were asked if hares were abundant, average, or scarce; and if hare numbers increased, decreased, or did not change from the previous winter. Responses numbered 140 to 256 yearly.

To investigate area differences in showshoe hare population levels, the Province of Alberta was divided into 9 geographic regions (Fig. 1). We calculated indices of hare abundance for each of these 9 regions. Abundance values of 1, 2, and 3 were assigned to the responses of scarce, average, and abundant, respectively. The following equation was then used to calculate the hare abundance index (I):

$$I = \left[\left(\sum_{i=1}^{n} R_i - n \right) / 2n \right] \times 100$$

where R_i is the numerical value assigned to the ith trapper response, and n is the number of trappers responding from a given region. This index thus expresses the cumulative response value of trappers in a given region as a percentage of the range of possible values. For example, if all trappers reported hares scarce, the index would be zero; if all reported hares abundant, it would be 100.

We assessed the reliability of this approach by comparing hare population indices calculated from responses of trappers in region 7 each winter with mean densities of hares (1 Dec) on 4 study areas within region 7 used for intensive studies of snowshoe hare populations
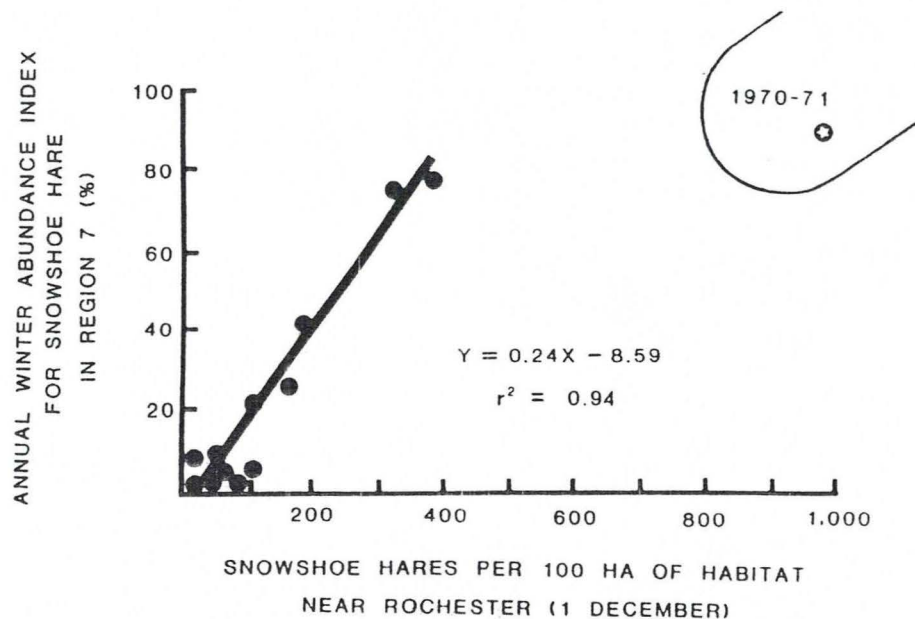
Fig. 2.   The relationship between estimated 1 December densities of snowshoe hares on 4 study areas near Rochester, Alberta (Keith et al. 1977; Keith, unpublished data) and hare-abundance indices calculatd from trapper questionnaires from region 7 (Fig. 1) during the winters of 1963–64 through 1975–76. Index for 1970–71 was excluded from regression analysis; see text for explanation.

near Rochester, Alberta (Keith et al. 1977). The relationship between the regional questionnaire index and hare densities on these 4 areas was linear ($r = 0.97$, df = 10) up to densities of about 400 hares/100 ha of habitat (Fig. 2). At that population level, most trappers reported hares abundant, and it was impossible for the index value to continue to increase in proportion to further increases in hare densities. Only during the peak winter of 1970–71 did densities exceed 400/100 ha. During the period covered by the present study (1971–72 through 1975–76), December hare densities at Rochester declined from 388 to 5/100 ha.

Lynx Carcass Collection.—Carcasses (1,108) were obtained from trappers in

Alberta during winters 1971–72 through 1975–76 (Fig. 1); 5 others were obtained by shooting or were recovered dead along a road. In 1971–72 all carcasses were obtained from the Swan Hills area in west-central Alberta (region 3); and in 1975–76 from Swan Hills and the High Level area in northwest Alberta (regions 1 and 2). During other winters, carcasses were obtained from trappers in all forested regions of Alberta except the area northeast of Desmarais (regions 5 and 6).

One hundred twenty-five trappers cooperated for 1 or more trapping seasons (1 Nov–28 Feb) by saving skinned lynx carcasses. This represented about 5% of the registered trappers in Alberta, and the reported catch comprised 5 to 6% of

the provincial lynx harvest during 1972–73, 1973–74, and 1974–75. Likewise, total trapline area of the cooperating trappers (21,650 km²) represented roughly 4% of an estimated 531,000 km² of lynx habitat in Alberta.

Lynx Diet.—Food habits were determined from remains in gastrointestinal tracts. Stomach and intestinal contents were weighed separately, and percent volume of each food item was visually estimated to the nearest 20%. Numbers and species of prey and carrion were identified from hair, bones, teeth, claws, feathers, or beaks. Lynx hair was commonly found in stomachs, but was not considered to represent food unless it was accompanied by bones and/or large chunks of flesh that we believed to be lynx. Reference collections in museums at the universities of Alberta and Wisconsin were used to help identify prey species.

Mean weights of prey species recorded by us at Rochester, or obtained from the literature, were multiplied by numbers present in each stomach or intestine to estimate prey biomass in the lynx diet. If prey weight exceeded that of a hare, for example beaver (*Castor canadensis*) and deer (*Odocoileus* spp.), we assumed that its occurrence represented a meal equivalent in biomass to 1 hare. This assumption was based on the fact that mean weight of carrion and/or larger prey in the stomachs of 21 lynx (167 + 87 g) was not statistically different from that in 205 stomachs containing 1 hare only (160 ± 28 g).

We were unable to separate remains of baits used by trappers from foods obtained during natural feeding by lynx. Hence there is a bias of unknown magnitude in our food-habits analysis. Although not all lynx sets are baited, trappers often use flesh and organs from a variety of skinned carcasses. If bait is consumed, however, its occurrence may not be recognized. Baits used by trappers may have reflected availability of foods normally utilized by lynx, as suggested by MacPherson (1969:19) for trapped arctic foxes (*Alopex lagopus*). The sample (5) of gastrointestinal tracts from lynx that were not trapped, and whose contents were thus not biased by use of bait, was too small for meaningful comparisons with trapped lynx.

Fat Reserves in Lynx.—Many methods have been used to describe the physical and nutritional status of wildlife, including weight-length relationships (Bandy et al. 1956, Bailey 1968), blood parameters (Bandy et al. 1957, Wilson and Hirst 1977), and estimates or measurements of stored fat (Cheatum 1949; Riney 1955; Ransom 1965; Flux 1970, 1971; Smith 1970; Caughley 1971).

We measured 2 indices of total body fat, renal and subcutaneous fat deposits, which we equated directly with nutritional status. These were evaluated visually on a scale of 1 (none) to 5 (very abundant).

Reproductive Performance of Lynx.—Female reproductive tracts were fixed in 10% formalin. Assessment of reproductive performance was based on corpora lutea and placental scars. Corpora lutea of previous pregnancies in lynx have been referred to as corpora albicantia (Saunders 1961, van Zyll de Jong 1963, Nava 1970, Stewart 1973), but Crowe (1975:186–187) pointed out that this is a misnomer in bobcats (*Lynx rufus*). Since luteal bodies of previous pregnancies appear similar in lynx to those in bobcats (Saunders 1961), we refer to these as corpora lutea, with the understanding that they are derived from both mature and degenerate (atretic) follicles of past breeding seasons (Mossman and Duke

1973:49). We interpreted the presence of corpora lutea as evidence of previous ovulations, thus sexual maturity. Counts of corpora lutea were used to assess ovulation rates.

From placental scars we determined implantation rates (percentage of females with implantation sites) and in utero litter sizes. We considered all individuals with implantation sites as having been pregnant, and thus equate implantation rate and pregnancy rate (percent females pregnant). Reproductive tracts were removed from the carcasses and held to a strong light; opaque areas in the uterine horns were counted as apparent implantation sites. This method of counting placental scars accurately reflected litter sizes among postpartum European foxes (*Vulpes vulpes*) of known reproductive history (E. K. Barth, personal communication cited in MacPherson 1969:29), and has been used to assess pregnancy in foxes (Layne and McKeon 1956, McEwen and Scott 1957, Englund 1970) and lynx (Saunders 1961, Nava 1970).

Age Determination of Lynx.—Ages over 1-year-old were determined by dark-staining layers, or annuli, observed in cementum of canine teeth. Canines were removed by boiling skulls. After storage in 10% formalin, the canines were decalcified in 5% HNO₃ until soft and sectioned longitudinally with a freezing microtome. Six to 12 sections of the canine root (15–20 μm thick) were stained with haemotoxylin as described by Nellis (1975), and observed under 100 power with a microprojector. This method of age determination has not been tested with lynx of known age. We found dark-staining layers similar in appearance to yearly annuli of bobcat and coyote (*Canis latrans*) teeth (Linhart and Knowlton 1967, Crowe 1972, Fritts 1973), and many other species (Klevezal and

Kleinenberg 1969). Nellis et al. (1972) found that teeth of 5 marked lynx whose minimum ages were known showed at least the minimum expected number of annuli.

The 1st annuli of bobcats and coyotes appear to be deposited at the periodontal-cementum interface toward the end of their 2nd winter, and subsequent annuli are laid down yearly. Lynx trapped in the present study during late January and February often had annuli juxtaposed to the periodontal-cementum interface. Thus deposition of annuli in lynx appears similar to that in bobcats and coyotes. For lynx trapped during January and February, we measured the distances of the most recent annulus from the periodontal-cementum interface. This was used to differentiate between currently growing annuli and those from the previous winter.

Lynx kittens (up to 1 year of age) were easily recognized by their large apical foramina in canine roots as described by Saunders (1963a). Closure of root canals is apparently complete by 14 months of age (van Zyll de Jong 1963).

RESULTS AND DISCUSSION
Trends in Snowshoe Hare Populations

Trapper responses to annual hare questionnaires from various regions of Alberta (Fig. 1) were compared. Chi-square contingency tables were used to test for differences in numbers reporting hares scarce, average, or abundant. Since lynx carcasses were not obtained from regions 5 and 6, responses from these regions were excluded from this analysis. Only 1 winter (1972–73) showed a significant difference in trapper responses between regions. During that winter, hares were apparently more abundant in regions 3
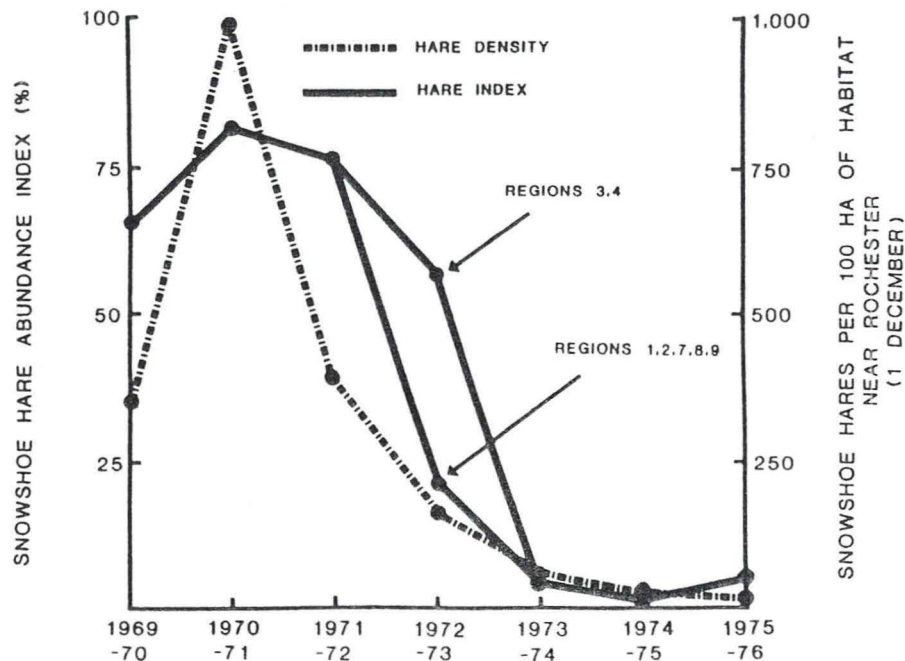
Fig. 3. Snowshoe hare abundance indices calculated from annual questionnaires to registered trappers in Alberta, and hare densities on 4 study areas near Rochester, Alberta (Keith et al. 1977; Keith, unpublished). Indices for regions 3 and 4 during 1972–73 were significantly greater than for regions 1, 2, 7, 8, and 9.

and 4 than elsewhere ($P < 0.001$). When there were no interregional differences in trapper responses for a given winter, questionnaire data were combined to depict the province-wide population.

The hare population in Alberta peaked during winter 1970–71, as did hares on the study areas at Rochester (Fig. 3). During the subsequent 5 years, the abundance index for all regions (Fig. 3) declined from 82 to 5%, and 1 December hare densities at Rochester fell from 990 to 5/100 ha of habitat. Between 1971–72 and 1972–73, the abundance index in regions 3 and 4 declined only from 80 to 57%, whereas in regions 1, 2, 7, 8, and 9 the index declined from 76 to 22%.

Interpreting the relationship between hare densities at Rochester and abundance indices in region 7 (Fig. 2), we classified hares as regionally *abundant* when index values exceeded 50%. This included all regions during 1971–72 and regions 3 and 4 during 1972–73. We interpreted regional indices between 20 and 50% as indicating hares at *intermediate* levels (regions 1, 2, 7, 8, and 9 during 1972–73), and indices below 20% as indicating hares *scarce* (all regions during 1973–74, 1974–75, and 1975–76).

Trends in Lynx Populations

Fur sales have been commonly used to index population trends of boreal preda-
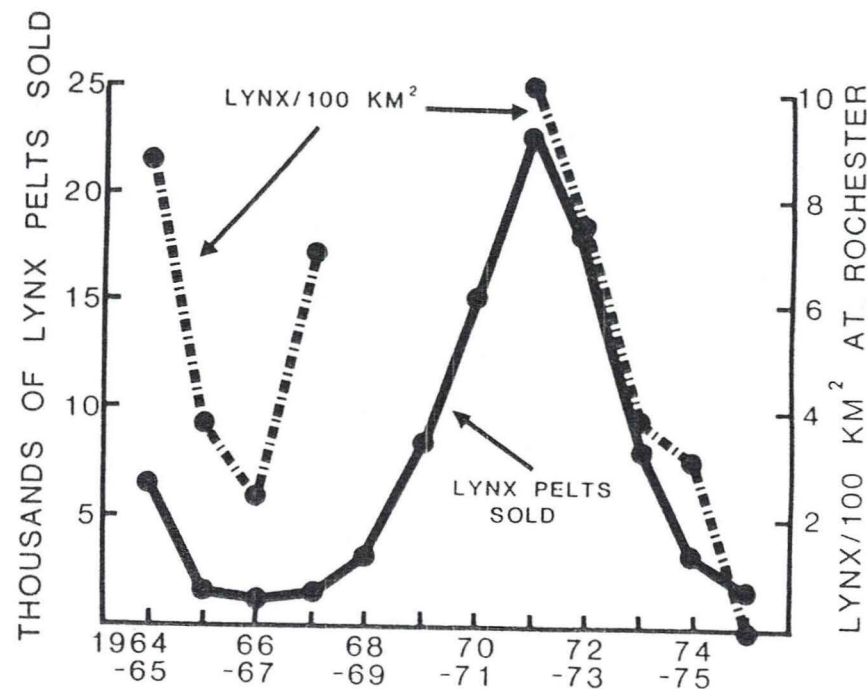
Fig. 4. Number of lynx pelts sold in Alberta (Statistics Canada 1973, 1975, 1977; A. W. Todd, personal communication) and lynx per 100 km² on a 130-km² study area at Rochester, Alberta (Brand et al. 1976) during 1964–75.

tors (Seton 1911, Hewitt 1921, Keith 1963, Bulmer 1974). The accuracy with which this index depicts amplitudes and timing of population fluctuations often has been questioned due to the potential influence of fluctuations in pelt value on trapping pressure, and the effect of varying levels of prey populations on the vulnerability of predators to trapping (Chitty and Chitty 1941:193, Elton and Nicholson 1942:242–243, de Vos and Matel 1952:743). Fluctuations in numbers of lynx pelts that were trapped and sold in Alberta did, however, parallel changes in lynx numbers on a 130-km² study area at Rochester (Fig. 4). Lows occurred in both fur returns and lynx densities during winters 1966–67 and 1975–76, while a peak

occurred in 1971–72 (Brand et al. 1976, Brand unpublished data). Between 1966–67 and 1971–72 the magnitude of change in fur returns was about 20-fold, whereas lynx densities at Rochester changed only 4.3-fold. Between 1971–72 and 1975–76, though, the number of lynx pelts sold in Alberta decreased 12.5-fold, while lynx numbers at Rochester decreased from 13 to 0.

Fur returns for Alberta thus accurately indexed the timing of a peak and 2 lows of the Rochester lynx population, but not its amplitude of fluctuation.

Food Items of Lynx

Lynx depend on the snowshoe hare during all phases of the hare's 10-year

Table 1. Percent occurrence and percent biomass of food items in 879 stomachs of lynx obtained during winter from trappers in Alberta at 3 levels of hare abundance.

Prey group	% occurrence[a] at different hare population levels			% biomass at different hare population levels		
	Abundant (72)[b]	Intermediate (114)	Scarce (338)	Abundant	Intermediate	Scarce
Snowshoe hare[c]	90	66	35	97	86	65
Red and flying squirrel		9	12		3	3
Mice and voles	4	7	28	<1	<1	1
Other rodents	1	4	5	1	6	8
Carnivores	1	3	3	1	2	5
Ungulates		2	3		2	5
Grouse		2	6		1	3
Other birds	3	6	6	3	2	4
Miscellaneous		2	4		<1	5

[a] Percent occurrence was calculated as number of occurrences of a species divided by total occurrences of all species.
[b] Number of stomachs excluding those that were empty; total numbers were 186, 228, and 465.
[c] Differences (*P* < 0.001) were found in the percent occurrence of snowshoe hare over 3 levels of hare abundance.

cycle of abundance (Saunders 1963*b*, van Zyll de Jong 1966, Nellis et al. 1972, Stewart 1973). Brand et al. (1976) described changes in use of hares by lynx, as determined from trailing during 6 winters of varying hare densities. Lynx diets determined from the trapped carcasses also changed with hare densities. Percent occurrence of hare in lynx stomachs decreased (*P* < 0.001) from 90 to 35% between years of hare abundance and scarcity (Table 1). Mice and voles comprised the only prey group whose occurrence increased significantly (from 4 to 28%) as hares became scarce, although utilization of all other food items increased to some extent. The change in percent biomass of hares in the lynx diet was from 97 to 65%. The large increase in percent occurrence of mice and voles was mitigated by their small individual biomass. No 1 alternative prey group predominated as percent biomass of hares decreased.

Rates of Consumption by Lynx

Brand et al. (1976) reported that the shift by lynx to alternative food sources as the hare population declined at Rochester (1971–72 through 1974–75) did not completely compensate for the decrease in biomass of hares killed per individual lynx; thus the mean daily consumption rate of individual lynx decreased 37%. We could not directly determine changes in consumption rates by lynx from our trapped sample. However, 3 potential indices of consumption rate (Table 2) were examined:

(1) The proportion of lynx intestinal tracts that contained food differed over the 3 levels of hare abundance (*P* < 0.01). At intermediate hare population levels, 78% of lynx intestinal tracts contained some food material, compared with 88% during years of both hare abundance and scarcity. This index thus yielded no consistent indication of decreased food intake at lower hare densities. The proportion of stomachs containing food was not considered because of the greater potential influence of baits on apparent ingestion prior to trapping.

(2) Weight of intestinal contents at time of necropsy differed (*P* < 0.001) between hare population levels. Mean biomass decreased from 45 g during

Table 2. Indices to rates of food consumption by lynx in Alberta during winter at 3 different levels of hare abundance. Sample sizes in parentheses.

Index	Hare population level			Probability of differences among levels
	Abundant	Intermediate	Scarce	
Percent intestines containing food material	88 (192)	78 (236)	88 (464)	<0.01[a]
Mean weight of intestinal contents (g)	45 (132)	33 (181)	31 (428)	<0.001[b]
Mean total live-weight of prey represented in intestine (g)	1,291 (168)	1,205 (185)	1,169 (405)	<0.03[b]

[a] Level of significance determined by chi-square test.
[b] Levels of significance determined by analysis of variance test.

hare abundance to 31 g during hare scarcity.

(3) By applying live weights of prey species to prey items in lynx intestines, we estimated the total biomass (before digestion) of food in the intestine. This index of biomass consumed also decreased (*P* < 0.03) between hare abundance and scarcity (from 1,290 to 1,170 g), but consumption during intermediate years did not differ from either (Duncan's Test). Complete passage of food through gastrointestinal tracts of domestic cats and bobcats takes 2–4 days (Hoelzel 1930:476, Petrides 1968), although the rate is related to type of food, condition of animal, and degree of digestion (Petrides 1968:28). A. W. Todd, Alberta fur biologist, reported (personal communication) that trappers generally check lynx sets every 2 or 3 days, and that captured lynx are usually alive. Thus if lynx are in the trap an average of 1 to 1.5 days, food remains in the intestine would represent items eaten 0.5–2.5 days prior to capture.

Two of the above 3 indices applied to food consumption by lynx declined with hare scarcity, as did estimates of food consumption obtained earlier by trailing lynx at Rochester (Brand et al. 1976).

Fat Reserves of Lynx

We examined the interrelationships between our indices of subcutaneous and renal fat by correlation analysis within categories of sex, age, hare abundance,

Table 3. Mean indices to renal and subcutaneous fat deposits for lynx collected from trappers during early (1 Nov–15 Jan) and late (16 Jan–28 Feb) winter at 3 levels of hare abundance. Sample size in parentheses.

Fat index[a]	Sex or age	Early winter			Late winter		
		Abundant	Intermediate	Scarce	Abundant	Intermediate	Scarce
Renal fat[b]	Yearling	2.5 (26)	3.0 (41)	2.8 (51)	3.2 (52)	3.5 (76)	2.7 (59)
	Adult	2.6 (19)	3.6 (12)	2.9 (93)	3.6 (33)	3.9 (30)	2.4 (231)
Subcutaneous fat[c]	Male	2.6 (28)	2.9 (41)	2.7 (70)	3.2 (57)	3.4 (79)	2.3 (154)
	Female	2.2 (26)	2.6 (32)	2.6 (88)	2.8 (53)	3.1 (59)	2.1 (170)

[a] Fat indices were evaluated visually on a scale of 1 (none) to 5 (very abundant).
[b] Renal fat was affected by age (*P* < 0.03), hare abundance (*P* < 0.001), season (*P* < 0.001), and an interaction between hare abundance and season (*P* < 0.001).
[c] Subcutaneous fat was affected by sex (*P* < 0.001), hare abundance (*P* < 0.001), season (*P* < 0.003), and an interaction between hare abundance and season (*P* < 0.001).

and season (1 Nov–15 Jan and 16 Jan–28 Feb). Correlations between these indices were all positive ($P < 0.05$, r values ranged from 0.59 to 0.86), suggesting a common relationship to total body fat. Both renal and subcutaneous fat indices showed effects of hare abundance ($P < 0.001$) and season ($P < 0.004$), and an interaction between hare abundance and season ($P < 0.001$). Renal fat was affected by age ($P < 0.03$), while subcutaneous fat was affected by sex ($P < 0.001$).

Renal Fat Index.—Renal fat indices among yearlings were consistently less than among adults, except during late winters of hare scarcity (Table 3). Growth in lynx continues through at least 2 years of age (Saunders 1963a, van Zyll de Jong 1963): the lower fat reserves of yearlings may be caused by their energy requirements for growth.

Renal fat indices during early winter were greatest at intermediate hare levels, but were similar during abundant and scarce hare levels, suggesting that renal fat was not related to early-winter hare abundance. Renal fat indices during late winter were also greater when hare populations were intermediate. There was, however, a large decrease in fat indices among both yearlings and adults during late winters of hare scarcity. This would explain the observed statistical interaction between hare abundance and season.

Subcutaneous Fat Index.—Subcutaneous fat was consistently greater among males than females (Table 3). Trends in subcutaneous fat were related to hare abundance and season. Greatest index values occurred at intermediate levels of hare abundance, with a marked decrease late in winters of hare scarcity.

It appeared that hare abundance affected only renal and subcutaneous fat during late winter. The decrease in late-

winter fat during years of hare scarcity suggested that a negative energy balance accompanied the reduced consumption rates recorded by us at such times.

Reproductive Performance of Lynx

Decreases in all assessed reproductive parameters (ovulation rates, pregnancy rates, and litter sizes) occurred between years of hare abundance and scarcity. We believe that these decreases were directly related to nutrition. Nutrition has been shown to play an important role in reproduction of wild mammals (Sadleir 1969). Slower growth rates of young caused by inadequate nutrition can delay the age at which sexual maturity is reached. Among mature females, decreased reproductive output due to malnutrition may be reflected in nonbreeding, reduced ovulation and pregnancy rates, and/or increased prenatal mortality.

Ovulation Rates.—Ovulation rates were directly related to hare population levels. Crowe (1975:187) suggested that corpora lutea of previous pregnancies in bobcats are retained throughout life, though those from different breeding seasons can be distinguished by color (Duke 1949, Gashwiler et al. 1961). Among lynx, corpora lutea also appear to persist for more than 1 breeding season (Nellis et al. 1972), but we were unable to distinguish those from different breeding seasons by color. While a direct comparison of ovulation rates in relation to hare abundance was thus impossible among adults, we were able to indirectly assess changes in adult ovulation rates.

When hares were abundant, 61% of 143 yearling female lynx ovulated during their 1st year, as indicated by occurrence of corpora lutea; the mean number of corpora per ovulating female was 5.1 ± 0.3. We were unable to test the relationship of percent yearlings ovulating to decreas-

Table 4. Mean numbers of corpora lutea[a] among female lynx collected from trappers in Alberta, but including only lynx born during years of hare abundance. Sample sizes in parentheses.

Age (years)	Mean ± 95% CI of corpora lutea per female during each reproductive season				Probability of differences among years[b]
	1972	1973	1974	1975	
1	5.5 ± 0.7 (59)	4.3 ± 0.8 (29)			<0.05
2	7.3 ± 1.6 (25)	6.8 ± 1.2 (43)	4.4 ± 0.8 (18)		<0.025
3	9.8 ± 3.7 (8)	11.9 ± 2.5 (13)	5.5 ± 1.1 (28)	5.6 ± 3.1 (8)	<0.001
4	11.2 ± 2.2 (4)	11.8 ± 6.2 (5)	9.2 ± 1.9 (13)	7.6 ± 2.8 (8)	NS

[a] Corpora lutea include luteal bodies of previous pregnancies, as discussed in text.
[b] Levels of probability determined by analysis of variance.

ing hare populations because of small sample sizes. Other lynx studies, however, suggested that the age of attainment of sexual maturity, as indicated by corpora lutea, was influenced by hare abundance. Saunders (1961:54) reported that during hare scarcity in Newfoundland, females did not breed until their 2nd year; while Nava's (1970:88) data from Alaska indicated a significantly higher percentage of yearlings with corpora lutea in areas where hares were abundant (91%) than where hares had begun to decline (83%).

If we assume that a constant percentage of female lynx born during years of hare abundance ovulated during their 1st year, then changes in the mean number of corpora lutea within each adult age class during subsequent years may reflect changes in ovulation rates. Table 4 shows the mean number of corpora lutea for each age-class by reproductive year. Only cohorts born during hare abundance, and thus presumably experiencing similar ovulation rates during their 1st year, are included. The partial accumulation of corpora lutea from different breeding seasons can be seen in the rising trend in mean number with age. For example, during 1972, average numbers of corpora lutea per female increased from 5.5 (yearlings) to 11.2 (4-year-olds). The mean increment in numbers of cor-

pora between successive age classes (2.1) was less than expected if all had been retained over the years; apparently some became indistinguishable with age.

Using separate analyses of variance for each age-class, we tested for year-to-year differences in mean number of corpora lutea per ovulating female born during years of hare abundance. Among yearlings, numbers of corpora lutea decreased ($P < 0.05$) between 1972 (5.5) and 1973 (4.3). In 2 of the 3 adult age-classes, mean numbers of corpora lutea also decreased (Table 4); from 7.3 to 4.4 among 2-year-olds during 1972–74 ($P < 0.025$), and from 9.8 to 5.6 among 3-year-olds during 1972–75 ($P < 0.001$). The observed decrease from 11.2 to 7.6 among 4-year-olds was not statistically significant because sample sizes were small during 1972 and 1973. Such changes in ovulation rates can be caused by changes in the percent females ovulating and/or the number of ovulations per female. Since both pregnancy rates and in utero litter sizes determined by placental scars decreased significantly with decreasing hare abundance (discussed later), we suspect that both factors were involved.

Pregnancy Rates and Litter Sizes.— Pregnancy rates of yearling lynx could be determined only during years of hare abundance (Table 5). The rate of 40% among yearlings at such times was less

Table 5. Pregnancy rates and in utero litter sizes of yearling and adult lynx collected from trappers in Alberta according to 3 levels of hare abundance. Sample sizes in parentheses.

Reproductive parameter	Hare population level			Probability of differences among years
	Abundant	Intermediate	Scarce	
Pregnancy rate[a]				
Yearling	40% (129)	0% (6)	0% (3)	
Adult	73% (78)	46% (26)	33% (100)	<0.001[b]
Mean ± 95% CI of in utero litter size				
Yearling	3.9 ± 0.2 (129)			
Adult	4.6 ± 0.4 (78)	3.9 ± 0.7 (26)	3.4 ± 0.3 (100)	<0.005[c]

[a] Percent females with placental scars, as determined from uncleared reproductive tracts.
[b] Probability determined by chi-square test.
[c] Probability determined by analysis of variance.
* Denotes difference ($P < 0.001$) as determined by chi-square.
** Denotes difference ($P < 0.025$) as determined by analysis of variance.

than the 73% among adults ($P < 0.001$). Adult pregnancy rates decreased ($P < 0.001$) to only 33% in years of hare scarcity.

In utero litter sizes differed ($P < 0.025$) between yearling and adult lynx during years of hare abundance (3.9 ± 0.2 vs. 4.6 ± 0.4) (Table 5); and litter sizes of adults decreased ($P < 0.005$) to 3.4 ± 0.3 as hares became scarce.

Sex Ratios

Previous studies have shown that sex ratios among trapped lynx often favored males. Van Zyll de Jong (1963:5) reported a significant deviation (29 ♂♂:14 ♀♀) in "unfavorable habitats" (agricultural and settled areas) during 1961–63 in Alberta, and suggested that this was due to greater mobility of yearling males as a result of "high population pressure." However, the sex ratio (41 ♂♂:25 ♀♀) in a sample from elsewhere in Alberta and the Northwest Territories in these same years was not significantly different from the above ratio or from equality. The overall sex ratio (71 ♂♂:39 ♀♀) differed significantly from 50:50. Stewart (1973:17) found a sex ratio of 21 ♂♂:4 ♀♀ among yearling lynx trapped in Ontario during 1971–72, and Berrie (1974:28) also reported a deviant sex ratio of 231 ♂♂:160 ♀♀ in a trapped sample from Alaska during 1969–70. Such disparities in sex ratios may reflect sex-specific trap biases, as suggested for bobcats in Arkansas (Fritts 1973:46), but actual sex ratios of lynx populations were unknown.

We tested sex ratios among trapped lynx during the present study according to age class (kitten, yearling, adult), level of hare abundance, and season. There was no significant deviation from 50:50 in any of the above 18 tests; the overall sex ratio of 974 lynx was 48 ♂♂:52 ♀♀.

Lynx Age Distribution

Changes in the age distribution of lynx collected from trappers each winter from 1971–72 through 1975–76 are presented in Table 6. Data from 1972–73 are combined separately for regions 3 and 4 and for regions 1, 2, 7, 8, and 9 because of the interregional differences in hare population levels.

The proportion of kittens in trapped samples decreased from 31% during 1971–72 (sample available from region 3 only) to 18% in regions 3 and 4 during 1972–73. In other regions, where hare

Table 6. Age distributions of lynx carcasses collected from trappers in Alberta from 1971–72 through 1975–76. Sample size is shown in parentheses.

Age (years)	1971–72* (52)	1972–73		1973–74 (284)	1974–75 (202)	1975–76 (32)
		Regions 3 and 4 (180)	Regions 1, 2, 7, 8, 9 (223)			
Kitten	31	18	7	<1		
Yearling	54	48	67	44	1	12
2	6	22	16	41	29	6
3	6	7	4	11	49	44
4	2	2	2	3	13	34
5+	2	3	4	1	7	3
$\bar{x}$	1.6	1.9	1.9	2.3	3.5	3.6
Hare abundance index (%)	77	57	22	5	2	5

* Lynx collected during 1971–72 were from region 3.

populations were even lower in 1972–73, only 7% of the lynx carcasses were kittens. During the 3 years of hare scarcity (1973–74 through 1975–76), just 1 kitten appeared in our carcass collections (during 1973–74).

Accompanying this decrease in recruitment was a progressive shift in population age distribution toward older cohorts, e.g., during 1973–74 85% of trapped lynx were yearlings and 2-year-olds; during 1974–75 78% were 2- and 3-year-olds; and during 1975–76 78% were 3- and 4-year-olds. Mean age of trapped lynx thus rose from 1.6 years in 1971–72 to 3.6 years in 1975–76.

Changes in age structure of trapped lynx have been reported in Alaska (Berrie 1974:28), where the proportion of kittens increased from zero (1966–67) to 30% (1969–70) with increasing hare densities. W. H. Koonz (personal communication) found a decrease, as we did, in the proportion of lynx kittens trapped in Manitoba during the last hare decline (40% in 1971–72 to 2% in 1973–74).

Three factors suggested that age distributions of trapped lynx did not accurately reflect actual population age distributions:

(1) We compared the kitten:adult ratio among trapped lynx during the population peak of 1971–72 with that of an hypothetical age-stable population after 5 consecutive years of increase. A population with constant age-specific birth and mortality rates will rapidly approach a stable age distribution regardless of whether the population is increasing or decreasing (Lotka 1922). We suspect that when hare populations were increasing during 1966–71, conditions were favorable for high and constant birth rates in lynx. To calculate hypothetical stable age distributions for 1971–72, we combined age-specific natality rates recorded during years of hare abundance with age-specific mortality rates ranging from 20 to 60% annually for kittens and 20 to 50% for adults. Because mortality rates of lynx during cyclic increases are unknown, these mortality rates are those that, under the above reproduc-

Table 7. Estimates of age distributions among lynx populations in Alberta, as determined by adjusting age ratios of trapped lynx to account for under-representation of kittens (see text for explanation). Adjusted sample sizes are shown in parentheses.

Age (years)	1971–72 (106)	1972–73		1973–74 (301)	1974–75 (215)	1975–76 (34)
		Regions 3 and 4 (264)	Regions 1, 2, 7, 8, 9 (370)			
Kitten	66	53	22	3[a]	3[a]	3[a]
Yearling	26	28	58	43	1	12
2	3	13	14	39	28	6
3	3	4	3	11	48	42
4		1	2	3	13	33
5+	2	1	1	1	7	3
$\bar{x}$	1.0	1.3	1.7	2.2	3.4	3.5

[a] Calculated as the mean percent kittens present during 1973–74 and 1974–75, as discussed in text.

tive schedule, resulted in a population increase of 4- to 2-fold over 5 years. Lynx populations at Rochester increased 4.3-fold from 1966–67 to 1971–72 (Brand et al. 1976), while fur-harvest figures changed 20-fold. In all of the above hypothetical populations, stable age distributions were achieved within 5 years; kitten:adult ratios ranged from 40:60 to 64:36. The observed age ratio in the trapped sample during 1971–72 (31:69) was less ($P < 0.05$) than hypothetical age ratios of 45:55 and greater. The percentage of kittens in the 1971–72 trapped sample thus appeared to underestimate the expected by about 20 to 50%.

(2) Kitten:adult ratios of lynx populations on a 130-km² area at Rochester were 7:6 (54% kittens) during 1971–72 and 4:6 (40%) during 1972–73 (Brand et al. 1976). The percentage of kittens in trapped samples (31 and 7%, respectively) in Alberta underestimated the corresponding percentages at Rochester by 43 and 82. During the subsequent 3 years, however, there were no kittens present either in trapped samples or at Rochester. Though this information is limited,

lynx populations at Rochester offered the only unbiased estimates of kitten:adult ratios currently known to us.

(3) Kittens born during 1974 were not represented in the 1974–75 carcass collection, yet the same cohort comprised 12% of the 1975–76 sample (as yearlings); again suggesting that kittens were underrepresented in trapped samples. A possible explanation for this underrepresentation of kittens is the continued partial dependence on their mother for food during the 1st winter (Saunders 1963c, Brand et al. 1976).

We estimated true age distributions of lynx populations from ratios in the trapped sample. Assuming that mortality rates between the 1st and 2nd winters of life are similar each year to rates among older individuals, the percent yearlings in the carcass collection for a given winter (kittens excluded) should depict the percent kittens during the previous year. We calculated percent kittens from percent yearlings in the following year. We combined 1974–75 and 1975–76 because of the small sample size during 1975–76. Age distributions were then adjusted to

correspond to the estimated percent kittens in lynx populations (Table 7). The adjusted age distributions also showed the progressive shift toward older age-classes, with mean age rising from 1.0 to 3.5 years. The proportion of kittens decreased from an estimated 66 to 3% between years of hare abundance and scarcity.

Lynx Mortality Rates

We estimated rates of trapping and nontrapping mortality during 1964–67 and 1971–75 from a population model using lynx densities at Rochester, provincial fur-harvest data, and information from the present study on reproduction and population age structure. The model was constructed as follows:

(1) Provincial lynx populations were estimated by extrapolating lynx densities determined by trailing on a 130-km² study area at Rochester (Brand et al. 1976) to the 531,000 km² of lynx habitat in Alberta. Such habitat included forested areas north and west of 54°N, 114°W. Since most trailing at Rochester was done during February and March, lynx densities there were regarded as depicting spring (post-trapping) populations. We do not know how representative these densities were of province-wide populations. There is, unfortunately, a paucity of information on lynx densities elsewhere with which to compare our estimates. Iurgenson (1955) estimated winter densities of European lynx (*Lynx lynx*) in the Central Zone, USSR, ranging from 1.7 to 5.6/100 km² between 1931–32 and 1949–50. This is about ½ the range of densities (2.3–10.0/100 km²) reported at Rochester by Brand et al. (1976), but on the other hand the European lynx is

about twice as large as the Canada lynx. Our estimates of lynx populations in Alberta ranged from 12,200 during the spring low in 1967 to 53,100 during the peak in 1972 (Table 8, columns B and G).

(2) Finite rates of reproductive increase (RI) among lynx populations during 1972, 1973, and 1974 were calculated from a modified equation for net reproductive rate (Krebs 1972:167) as follows:

$$RI = 1 + \frac{\left[\begin{array}{c}(P_k \times PR_k \times LS_k) \\ + (P_a \times PR_a \times LS_a)\end{array}\right]}{2}$$

where P refers to the estimated proportion of kittens (k) and adults (a) in the previous winter's lynx population, PR is the age-specific pregnancy rate (percent females pregnant), and LS is the mean in utero litter size (determined from placental scars). The proportion of kittens in lynx populations was obtained from our adjusted age distribution (Table 7); a 50:50 sex ratio was assumed. During 1965 and 1966, rates of reproductive increase were assumed to be similar to that in 1974, since hares were scarce during those years. Rates of reproductive increase (Table 8, column C) were then applied to our estimates of provincial lynx populations in spring to calculate population size immediately after births in May (Table 8, column D).

(3) The number of lynx pelts sold in Alberta (Statistics Canada 1973, 1975, 1977; A. W. Todd, personal communication) during the subsequent trapping season was subtracted from spring populations (after births) to obtain a theoretical population estimate for the following spring (before births) (Table 8, column F). The dif-

Table 8. Estimates of annual rates of trapping and nontrapping mortality among lynx populations in Alberta during 1964–67 and 1971–75.

Biological year (May–May)	A Lynx per 100 km² Rochester[a]	B Estimated lynx population in May (before births) A × 531,000 km²[b]	C Finite rate of reproductive increase[b]	D Lynx population in May (after births) B × C	E Total lynx trapped over winter[c]	F Remaining lynx[d]	G Lynx population in following May (before births)[e]	H Nontrapping mortality rate (%) (May–Nov) (F – G)/F × 100	I Trapping mortality rate (%) (Nov–Mar) E/D (F – G) × 100
1964–65					6,495		45,100		13
1965–66	8.5	45,100	(1.5)[f]	67,650	1,638	66,012	20,200	68	8
1966–67	3.8	20,200	(1.5)[f]	30,300	1,098	29,202	12,200	56	8
1971–72					22,776		53,100		30
1972–73	10.0	53,100	2.4	127,440	18,084	109,356	40,900	54	31
1973–74	7.7	40,900	1.8	73,620	8,056	65,564	20,200	62	29
1974–75	3.8	20,200	1.5	30,300	3,445	26,855	16,500	34	17

[a] Data from Brand et al. (1976)
[b] See text for calculations of reproductive increase.
[c] Data from Statistics Canada (1973, 1975, 1977) and A. W. Todd (personal communication).
[d] The theoretical number of lynx present in May if all mortality was due to trapping
[e] Column B of subsequent row.
[f] Reproductive increase for 1965 and 1966 was assumed similar to that observed during 1974, since hare population levels were similar.

ference between this theoretical population estimate and the corresponding spring population estimate determined independently from Rochester lynx densities thus equals the number of lynx dying from nontrapping mortality.

(4) The fall (pretrapping season) lynx population was calculated as the difference between spring (after births) estimates and the number dying from nontrapping mortality. We assumed here that all nontrapping mortality occurred prior to the trapping season. This assumption is supported by the fact that lynx population changes during the decline at Rochester occurred before winter (numbers did not change over winter) (Brand et al. 1976), and that age distributions of trapped lynx (Table 7) indicated that kittens disappeared before winter during years of hare scarcity.

(5) Rates of nontrapping mortality (Table 8, column H) are expressed as numbers of lynx dying from May to November divided by the May (after births) population estimate; the trapping mortality rate (Table 8, column I) is the number trapped divided by the fall population estimate.

Nontrapping Mortality Rates.—Estimates of nontrapping mortality rates from May to November were similar in 4 of 5 years, ranging from 54 to 68%; during 1974, nontrapping mortality dropped to 34% (Table 8). As previously noted, we assumed that nontrapping mortality occurred prior to the trapping season. There was no consistent relationship between nontrapping mortality and May population size, either before or after births.

We estimated numbers of kittens born each May from rates of reproductive increase and spring population size (Table 8, columns C and D). We then estimated the number of kittens in fall from winter age ratios and fall populations (Tables 7 and 8). This enabled us to calculate May-to-November mortality rates for kittens and adults in 1972, 1973, and 1974 (Table 9). These rates were 65, 95, and 88% for

Table 9. Estimates of nontrapping (May–Nov) mortality rates among kitten and adult lynx in Alberta during 1972–74.

Year	A N kittens born in May[a]	B N adults present in May[b]	C N kittens present in November[c]	D N adults present in November[d]	Kitten mortality (%) (May–Nov) (A – C)/A	Adult mortality (%) (May–Nov) (B – D)/B
1972	74,340	53,100	26,000	33,000	65	38
1973	32,720	40,900	1,700	26,600	95	35
1974	10,100	20,200	1,200	18,700	88	7

[a] Calculated from Table 8 as B × (C – 1).
[b] Table 8, column B.
[c] Calculated as percent kittens (Table 7) times fall population estimate [D – (F – G); Table 8].
[d] Calculated as percent adults (Table 7) times fall population estimate [D – (F – G); Table 8].

kittens, and 38, 35, and 7% for adults. The consistently high kitten mortality during the cyclic decline, coupled with decreased reproduction, accounted for the sharp drop in recruitment to winter populations; kitten mortality before winter averaged about 3 times adult mortality.

Trapping Mortality Rates.—Trapping mortality overwinter 1964–65 through 1966–67 averaged 10% of fall lynx populations (Table 8). During 1973–74 and 1974–75, when population levels were similar to 1965–66 and 1966–67, trapping mortality rates were 2 to 4 times greater (17 and 29%). The price of lynx pelts from Alberta averaged $44 during 1965–67, but $101 during 1972–75. Our conversations with trappers indicated that these higher pelt prices increased trapping pressure on lynx. We believe this probably led to the increased rate of harvest noted above.

During 3 years of consistently high pelt prices (1972–75), trapping mortality appeared density-dependent, decreasing from 31% of a fall population of 59,000 (Table 8, columns E and G) to 17% of 20,000.

Because we do not know the extent to which lynx densities at Rochester depicted provincial densities, and hence provincial population estimates, we also calculated minimum and maximum trapping mortality rates for each year by ad-

justing population estimates (Table 8, columns B and G) by 50% upwards and downwards, respectively. Resulting trapping mortality rates ranged from an average of 7 to 20% during 1964–67 and 20 to 42% during 1971–75.

Interactions Between Trapping and Nontrapping Mortality.—If trapping and nontrapping mortality are compensatory, we would expect a negative relationship between them. Regression analysis of trapping vs. nontrapping mortality during 1965–67 and 1972–75 showed no significant relationship ($P = 0.88$). During 1965–66 and 1966–67, when trapping mortality was 8%, nontrapping mortality rates (68 and 56%) were similar to those in 1972 and 1973 (Table 8); but trapping mortality in 1972–73 and 1973–74 was about 3 times greater (31 and 29%) than in 1965–66 and 1966–67.

We suspect that trapping pressure on lynx was directly related to pelt price, and within the framework of relatively high pelt price (1973–75) trapping mortality was density-dependent, as previously noted. Multiple regression of trapping mortality rates on mean pelt price and fall population estimates were not significant, but suggestive, because partial correlation coefficients were 0.56 ($P = 0.15$) and 0.66 ($P = 0.12$), respectively. If nontrapping and trapping mortality were unrelated, we might expect that a similar

multiple regression using nontrapping mortality rates would yield smaller partial correlation coefficients. This was the case, with corresponding correlation coefficients being −0.58 and 0.35 ($P = 0.34$ and 0.58).

These limited data suggest that rates of trapping and nontrapping mortality were not related; hence we suspect that trapping mortality is largely additive to nontrapping mortality.

MANAGEMENT IMPLICATIONS

It has long been contended that cyclic declines of lynx populations are ultimately caused by cyclic declines of snowshoe hares. They correspond closely in their respective fluctuations, and lynx depend heavily on hares as their major food source (Seton 1911:96–98, Hewitt 1921, Sheldon 1930:329, Elton and Nicholson 1942). We have concluded that the immediate cause of lynx declines is an absence of recruitment of kittens to winter populations together with continued adult mortality.

Caughley (1977:197–198) discussed 2 strategies for harvesting populations in a fluctuating environment: the "mean strategy" and the "tracking strategy." In the former, the variability of population size is ignored, and the rate of harvest is determined from the average size of the population. In the latter, rates of harvest change directly with rates of population increase (r); harvesting is curtailed when r is negative. Caughley aptly pointed out that when the mean periodicity of fluctuations exceeds 5 years, a tracking strategy is the only workable one. A tracking strategy is thus applicable to long-term management of lynx populations, where recruitment is absent or negligible for a period of 3 or 4 years during an 8- to 11-year cycle of abundance.

We believe that the predictability of

the following demographic events in the 10-year cycle of lynx populations provides a simple index to their status, and can be used as a sound basis for management decisions: (1) lynx populations and fur harvests reach a cyclic peak 1–2 years after cyclic peaks of snowshoe hares, and (2) recruitment of kittens to winter populations decreases dramatically 2 years after the peak in lynx fur harvest, and remains near zero during the next 3–4 years. Caughley's tracking strategy would entail curtailment of lynx trapping during these 3–4 years.

We investigated the long-term effect of a 3-year curtailment of lynx trapping on subsequent population levels and harvests using 2 hypothetical models. Both followed lynx populations from 1973–74 to the next projected population peak. In Model A, trapping mortality continued as described below; in Model B, trapping was discontinued during 1973–74 through 1975–76, i.e., when recruitment was near zero.

In both cases we assumed that minimum populations were reached in spring 1976, and subsequently increased for 5 years to peak levels in 1981. The finite rate of reproductive increase (RI) during the population increase was taken as 2.4 yearly, i.e., the rate recorded during hare abundance (Table 8). Because lynx numbers at Rochester increased 4.3-fold during 1966–67 to 1971–72, the annual finite rate of population increase (λ) was 1.34. We assumed that λ was constant and similar in each model population during the 5 increase years. The annual mortality rate (q_r) was thus calculated as:

$$q_r = [1 - (\lambda/RI)] \times 100,$$

or 44%.

We do not know the relative importance of trapping vs. nontrapping mortal-

Table 10. Population estimates and harvest data for lynx in Alberta during 1973–74 to 1980–81 as calculated from 2 hypothetical models. In Model A, trapping continued over the 8-year period; in Model B, trapping ceased during the 1st 3 years when recruitment to the population was near zero. See text for explanation of assumptions and calculations.

Model	May 1973 population estimate[a]	May 1976 population estimate	N lynx trapped (1973–76)	Projected N May 1981 population estimate[b]	Projected N lynx trapped (1977–81)	Total N lynx trapped (1973–81)
A	58,984	13,600	13,332[c]	58,760	28,900	42,232
B	58,984	27,700	0	119,675	58,900	58,900

[a] Data from Table 8.
[b] We assumed that lynx populations reach a cyclic low in 1976, then increased 4.3-fold over the subsequent 5 years to a peak in 1981.
[c] Data from Statistics Canada (1975, 1977).

ity during the lynx population increase. However, nontrapping mortality during 1972–75 averaged 50%, or 79% of total mortality (Table 8). We thus assumed that nontrapping mortality during the increase likewise comprised 79% of total mortality, or 35% annually.

By fixing rates of increase and nontrapping mortality, trapping mortality was also constant by necessity. Trapping mortality during the cyclic decline of 1972–75 appeared density-dependent within the framework of relatively high pelt prices, though this relationship is yet uncertain. During the cyclic increase, though, we do not have evidence that trapping mortality was density-dependent. These above assumptions provide a crude method by which we can predict long-term fur harvests and population trends.

Model A.—Our estimate of the Alberta lynx population in spring 1975 was 16,500 (Table 8). The assumption that rates of reproductive increase and mortality in 1975–76 were similar to those in 1974–75 gave a population in spring 1976 of 13,600 (Table 10). By thereafter applying an annual finite rate of increase of 1.34 (given above) we arrived at a population in spring 1981 of 58,760.

We calculated that during 1973–81 42,232 lynx would be trapped in Alberta (Table 10). This figure was based on ac-

tual harvest data from 1973–74 through 1975–76 (years of population decline), and estimated harvests from 1976–77 through 1980–81 (years of population increase). The latter were obtained by (1) subtracting a 35% nontrapping mortality rate from postbirth spring populations to estimate fall populations, and (2) determining the difference between fall and subsequent prebirth spring populations. Trapping mortality, as calculated above, amounted to 14% of fall numbers during the 5 increase years.

Model B.—Since trapping appeared additive to nontrapping mortality of lynx during their decline, we used only nontrapping mortality rates (Table 8) in calculating the numerical decrease from 1973 to 1976 in the absence of trapping. The resulting population estimate for spring 1976 was 27,700 (Table 10), or about twice the 13,600 predicted by Model A. If, on the other hand, trapping mortality were partly compensatory, data from Table 8 could be similarly used to predict other hypothetical spring populations. For example, if trapping mortality were 50% compensatory (50% of trapped lynx would have otherwise died during winter from nontrapping mortality), the 1976 population would be 19,800, approximately 1.5 times that given by Model A.

During the subsequent 5 years of in-

crease, the Model B population attained a peak of 119,675 compared to 58,760 for Model A. We assumed that below this level, social restriction of population size did not occur. Population regulation through social restrictions has been reported in the mountain lion (*Felis concolor*) (Hornocker 1969:464, Seidensticker et al. 1973:59) and wolf (*Canis lupus*) (Mech 1970:320), but these species rely on relatively stationary prey populations. We (Keith 1974:35, Brand et al. 1976:428) contend that certain predators, notably the arctic fox and lynx, which rely heavily on fluctuating prey populations do not exhibit such social restrictions to population size in the context of densities achieved in the field. Thus, while the relative size of the 2 hypothetical populations was the same in 1981 as in 1976 (2:1), the difference between them by 1981 was 60,100.

Under Model-B management, the estimated number of lynx trapped during the 5 increase years was 58,900; this compares to 28,900 for Model A. Total numbers of lynx trapped during 1973-81 would be 58,900 and 42,200, respectively; a net gain of about 16,700 for Model B even though it would eliminate trapping for 3 years during the population decline.

These models are crude, but they illustrate how, by curtailing lynx trapping during 3 years of the population decline, long-term lynx harvests can be increased. We thus suggest that lynx population trends be monitored through examination of annual fur harvests. During the 2nd winter after the fur-harvest peak, recruitment of kittens likely will drop sharply. Lynx trapping should then be curtailed for 3 or 4 years, i.e., until snowshoe hare populations recover sufficiently from their cyclic low to again permit lynx recruitment. Regional differences in

phases of the 10-year cycle would perhaps require management programs to be implemented on a regional rather than a state- or province-wide basis.

CONCLUSION

Holling (1959) described the numerical responses of predators to changing prey densities as stemming from dietary responses. Brand et al. (1976) found that lynx responded to changing hare densities at Rochester by shifting from hares to alternative food sources, and, more importantly, by varying food consumption rates. The present study indicated that similar dietary responses occurred among lynx throughout Alberta during the decline of 1971-76.

Indices of lynx body fat increased significantly between early and late winter when snowshoe hares were at intermediate or abundant levels, but decreased significantly during years of hare scarcity, suggesting that lynx experienced a negative energy balance. Brand et al. (1976) concluded that during years of hare scarcity, average consumption by lynx at Rochester dropped about 20% below that required to maintain body weight.

Lynx numbers at Rochester did not change overwinter during the population decline of 1972-75 (Brand et al. 1976). Since Rochester lynx populations were largely untrapped, it appears that disappearance of both kittens and adults occurred between the spring and winter. Nontrapping mortality factors of lynx are little known, but nutritionally stressed lynx, especially kittens, are probably more susceptible to mortality from disease, predation, and/or cannibalism as well as outright starvation. In addition, sibling aggression resulting from competition for food might occur among kittens, as reported among arctic fox pups (MacPherson 1969). Mortality of kittens

during hare scarcity occurs during summer and early fall when they are entirely dependent on their mother for food. Brand et al. (1976) reported from winter trailing at Rochester that kittens were present at only 7 of the 17 sites where kills were made by females with kittens. We do not know if the female shared the kill with her young in these cases, but we suspect she fed herself 1st.

Starving lynx are also probably more susceptible to human-related mortality during hare scarcity. Increased lynx movement in search of food may increase lynx-human contacts, especially in agricultural and other settled areas where alternative food may be more abundant. Undoubtedly, starving lynx are also attracted to baited sets. Outright starvation of lynx during contemporary lows in hare populations is likely less common than during pristine times.

Between years of hare abundance and scarcity, finite rates of reproductive increase among lynx decreased 38% (from 2.4 to 1.5, Table 8). This decrease, caused by reduced litter sizes and pregnancy rates, was partly responsible for the lack of recruitment to winter populations in decline years. Postpartum mortality of kittens before winter, however, removed 65 to 95% of the kittens born during the lynx population decline, and appeared mainly responsible for the lack of recruitment, as suggested by Nellis et al. (1972).

Mortality rates from trapping varied with pelt prices, and within the framework of consistently high prices, also appeared density-dependent. There was, however, no apparent relationship between trapping and nontrapping mortality. In the absence of trapping, lynx populations would hypothetically continue to decline during years of hare scarcity, but to levels above those of continuously trapped populations. This higher level

during the cyclic low would result in a greater overall harvest during the subsequent increase of the lynx population, and higher numbers at the peak.

Major increases in lynx pelt prices during the past 10 years have apparently increased trapping pressure; we have calculated that a 2- to 4-fold increase in rates of trapping coincided with a 2- to 3-fold increase in mean pelt value. Because trapping mortality appears additive to nontrapping mortality, intensive trapping could result in local extirpation of lynx during years when recruitment is absent. De Vos and Matel (1952) suggest that overtrapping of lynx was largely responsible for successively lower lynx population peaks in 1925-26, 1935-36, and 1944-45 across Canada. The geographical range of lynx was also decreasing during this interval when compared with the range reported by Seton (1929:157). If lynx pelt price continues at its recent high level, it is hoped that such a decline does not again occur.

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LYNX RESPONSES TO CHANGING SNOWSHOE HARE DENSITIES IN CENTRAL ALBERTA

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Abstract: Functional (dietary) and numerical responses by lynx (*Lynx canadensis*) to changing snowshoe hare (*Lepus americanus*) densities were studied by trailing lynx for 900 km during winter 1964–68 and 1971–75 at Rochester, Alberta. Lynx populations on a 130-km² study area responded numerically to changes in hare densities; the low of 3 in 1966–67 and apparent peak of 13 in 1971–72 followed by 1 year a respective low and subsequent peak among hares. There were no kittens present on the study area during five winters of greatest hare scarcity. Early postpartum mortality of kittens, probably starvation related, was at least partly responsible for the decline of lynx populations. Reduced conception rates among yearlings (again probably starvation-related) may have been additional factors in the decline, but their relative importance is still unknown. Lynx also responded functionally to changes in hare densities; frequency of hares in the lynx diet dropped to 5 of 13 food items during 1 winter of hare scarcity and rose to 16 of 17 items when hares were abundant. Carrion was the main alternative food source during the hare low in 1965–67. Ruffed grouse (*Bonasa umbellus*) was the only alternative prey species of importance to the lynx during hare lows. The mean daily consumption rate by adult lynx was 37 percent greater during winters of hare abundance than during winters of scarcity. Minimum estimates of home-range sizes (averaging 28.0 km²) did not appear related to either hare or lynx densities. Overlap of home ranges occurred in all years. Avoidance behavior appears to separate lynx in both time and space, but probably does not act locally as a density-limiting mechanism.

The cyclic fluctuations of lynx populations have been well-documented by fur returns since the early 1800's (Elton and Nicholson 1942). Their regularity and synchrony have been shown to reflect the "10-year cycle" of the snowshoe hare, the lynx's major food source (Keith 1963:65–66). Information on lynx population dynamics is still largely fragmentary and stems from short-term investigations. Saunders (1961, 1963*a, b*) studied the lynx in Newfoundland during 1956–61, from a low to a peak in hare numbers. Van Zyll de Jong (1963, 1966) studied lynx from 1961 to 1963 during a hare decline in Alberta and the Mackenzie District of the Northwest Territories. Nava (1970) obtained reproductive information from lynx carcasses collected in Alaska during 1964–65, a period of hare scarcity. The dynamics of lynx populations have not been studied through 1 complete 10-year cycle of abundance.

Our own investigation of lynx population dynamics began in 1964 at Rochester, Alberta. Its purpose was to investigate functional responses (changes in numbers of prey consumed by individual predators) and numerical responses (changes in predator density) of lynx to fluctuating hare densities (Solomon 1949, Holling 1959) and to measure rates of predation by lynx on major prey species. The study was divided into two phases. Results from the first phase (December 1964 to March 1968) were summarized by Nellis and Keith (1968) and Nellis et al. (1972); this first phase extended through a low to the early recovery of hare populations. The second phase (December 1971 to March 1975) was conducted over four winters during which the hare population declined from the cyclic peak of 1970–71. In this paper we examine functional and numerical responses by lynx as manifested in changing lynx densities, recruitment, home ranges, hunting behavior, and feeding habits in response to declining hare populations.

STUDY AREA

Our 130-km² study area was located near Rochester, Alberta, about 100 km north of Edmonton. Nellis et al. (1972:321) used a 148-km² study area during 1964–68, but we eliminated 18 km² of agricultural land because these were rarely used by lynx. Most movements of resident lynx were within the 70 km², so this arbitrary reduction of study-area size did not alter lynx numbers previously reported by Nellis et al. (1972). In 1972 the vegetation on this study area was approximately 33 percent improved pasture and cropland; 33 percent aspen (*Populus tremuloides*) and poplar (*P. balsamifera*) forest; 15 percent spruce (*Picea* spp.) forest; 8 percent bog with scattered black spruce (*P. mariana*), tamarack (*Larix laricina*), bog birch (*Betula glandulosa*), and willow (*Salix* spp.); 7 percent brushland with regenerating (post-fire) aspen, poplar, and willow; 2 percent marsh with cattail (*Typha latifolia*) and bulrush (*Scirpus* spp.); and 2 percent open water.

METHODS

Numbers of lynx on the study area were assessed from track observations and trailing. After snowfalls, all roads in the study area were driven each day and lynx tracks crossing roads were recorded until conditions prevented us from identifying recent tracks. We believe all lynx could be detected in this manner, because the study area contained a network of roads such that the largest unit not bisected by a road was one 4.8- × 3.2-km tract. Recent crossings were back-trailed to avoid flushing lynx from daytime beds; older tracks were forward- or back-trailed. Movements were plotted on a 4-inch-per-mile (1:15,840) cover map. A total of 900 km of lynx trails was plotted in the present study, 420 km during the first phase and 480 during the second.

We believe that we could determine accurately numbers of lynx and their movements on the study area from daily track observations along this network of roads and subsequent trailing of individuals to connect points where tracks were observed. The possible short-term occurrence of transient lynx may have been undetected by our method, however.

Lynx kittens reportedly remain with their mothers through the first winter (Saunders 1963*a*), dispersing in March at the onset of breeding. We assessed the presence of lynx kittens in winter populations from counts of family groups (adult female with kittens) travelling together. The tracks of kittens are noticeably smaller than those of adults. When trailing family groups, we followed only the adult female.

Winter food habits, hunting behavior, and hunting success were determined directly from trail sign. We noted kill attempts, number of jumps/attempt, distance/jump, and prey species. Percent

biomass of prey species in the lynx diet was calculated from prey-weight data recorded at Rochester. We assumed each visit to carrion constituted a meal equivalent to the biomass of one hare when the species weighed more than a hare, i.e., moose (*Alces alces*), white-tailed deer (*Odocoileus virginianus*), and domestic livestock. Mean live weights were applied to carrion species weighing less than one hare. This calculation of carrion consumption differed from that by Nellis and Keith (1968:722), wherein a meal of carrion was assumed to be 0.5 hare-equivalent. This change was made because the mean weight (153 g) of carrion and/or prey species larger than hare found in stomachs of 22 lynx collected from trappers in Alberta was similar to that of snowshoe hare (135 g) in 74 stomachs (Brand and Keith, unpublished data). We accordingly recalculated percent biomass estimates given by Nellis and Keith (1968).

Distance travelled daily was the trail-distance plotted between consecutive daytime beds, which appeared as ice-encrusted depressions in the snow where lynx bedded during the day. This distance is used in the present paper as an index to time and effort spent searching for prey.

Consumption rates (biomass consumed daily/individual) were calculated as the amount eaten between beds used on consecutive days. Estimates of carrion consumption and corrections for the proportion of each kill not consumed are included in this value. When kittens were present at a kill made by the mother, we calculated a minimum and maximum daily consumption rate for the adult female. Minimum consumption was estimated by dividing prey biomass equally among all lynx present at the kill; in estimating maximum consumption, we assumed the entire carcass was eaten by the female.

Snowshoe hare populations have been monitored within the lynx study area since 1961 (Meslow and Keith 1968, Keith, unpublished data). Methods of estimating hare population levels were discussed in detail by Meslow and Keith (1968). After a cyclic peak in fall 1961, December hare populations declined to a low of about 80/100 ha of hare habitat in 1965 and 1966 (Fig. 1). Hares subsequently increased peaking again in fall 1970 at about 1,700/100 ha. December densities then declined to 500 and 200 by 1971 and 1972; in 1973 and 1974 there were only 69 and 34 hares/100 ha of habitat, respectively. In assessing the effects of changing hare densities on lynx population dynamics, we hereafter refer to 1965–66, 1966–67, 1973–74, and 1974–75 as winters of hare scarcity (lows and 1964–65, 1967–68, 1971–72, and 1972–73 as winters of relative abundance (highs).

Ruffed grouse densities in December, estimated from monthly King strip-censuses (Keith, unpublished data), were about 86/
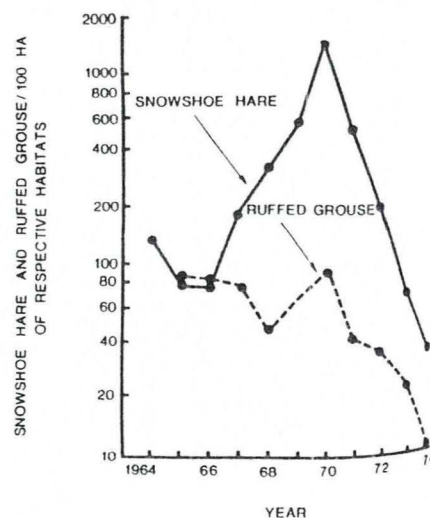
Fig. 1. Densities of snowshoe hares and ruffed grouse in December in respective habitats on four study areas near Rochester, Alberta. See text for habitat descriptions.

Table 1. Lynx numbers and densities during winter on a 340 km² study area at Rochester, Alberta.[a]

Year	No. adults	No. kittens	Lynx/ 100 km²	Hares/100 ha hare habitat[b] (1 Dec)
1964–65	11		8.5	137
1965–66	5		3.8	79
1966–67	3		2.3	80
1967–68	3	6	6.9	185
1971–72	6	7	10.0	499
1972–73	6	4	7.7	200
1973–74	5		3.8	69
1974–75	4		3.1	34

[a] Data for 1964–68 from Nellis et al. (1972).
[b] Hare habitat in the present paper is forest and brushland cover as discussed in text.

100 ha of habitat in 1965, 82 in 1966, and 79 in 1967. There were 40/100 ha in December 1971, 35 in 1972, 22 in 1973, and 10 in 1974 (Fig. 1).

RESULTS AND DISCUSSION

Numerical Response

Resident Lynx Densities.—Lynx numbers did not change over winter. The recurrence of lynx tracks at predictable locations throughout a given winter and subsequent connections of these locations by trailing suggested that these tracks were made by the same individuals or family groups. Thus it appeared that lynx populations at Rochester were resident individuals or family groups that remained on the study area over winter. This was borne out when a lynx whose track was identifiable due to a missing toe was trailed 98 and 132 km during 1965–66 and 1966–67, respectively, and used a well-defined "activity center" (Nellis et al. 1972).

Lynx densities at Rochester were related to hare abundance, but there tended to be a 1-year lag in population trends (Table 1). There were 8.5 lynx/100 km² in winter 1964–65, 3 years after the 1961–62 peak in lynx fur returns for Alberta (Nellis et al. 1972:322). Densities declined over the next

2 years to a low of 2.3/100 km² by winter 1966–67. This low followed the hare low by 1 year. Lynx densities increased to 6.9/100 km² in 1967–68, as hare populations began their recovery. We did not study the lynx population at Rochester between spring 1968 and fall 1971, but fur returns indicated they increased during these years to a provincial peak in 1971–72 (Statistics Canada 1972, 1973, 1974). The density of lynx at Rochester during winter 1971–72 was 10.0/100 km², 1 year after the fall 1970 peak in hare populations. Densities subsequently declined to 7.7 in winter 1972–73, 3.8 in 1973–74, and 3.1 in 1974–75. Hare populations also declined markedly during this period. The magnitude of change in lynx densities from the low in 1966–67 to the apparent high in 1971–72 was 4.3-fold.

Little information is available on lynx densities in other areas. Bergerud (1971:40) estimated densities in Newfoundland at 7.7/100 km² during 1964–65 (Middle Ridge) and 3.9/100 km² during 1965–66 (Avalon Peninsula). These estimates, based on removal trapping 4 and 5 years after an apparent hare peak in 1960, were twice the observed densities of 3.8 and 2.3/100 km² during comparable years in the hare cycle at Rochester (1965–66 and 1966–67). Bergerud (1971) noted that lynx at Middle Ridge were concentrated in an area of local hare abundance. He did not assess ingress during each removal period, and his figures perhaps overestimated resident densities.

Lynx Productivity.—During 1964–67, when December hare populations were 137, 79, and 80/100 ha of habitat, respectively, no kittens were present in winter (Table 1). Nellis et al. (1972:326) reported that ovulation had occurred in 15 of 17 female lynx collected in the Rochester district during these years. Parturition occurred on the study area at least in 1964 and 1966, as indicated by sightings of litters in summer

and from the condition of mammae of captured females that obviously had nursed young. Thus, Nellis et al. (1972) believed that the absence of kittens in winter populations during years of hare scarcity was primarily a function of early postpartum mortality. Two lynx litters with 3 kittens each were present throughout winter 1967–68, following a major increase in hare populations during summer 1967 to 185/100 ha of habitat in December.

During winter 1971–72, 1 year after the hare peak, there were 2 litters of 3 and 4 kittens; hare density was 499/100 ha of habitat. Three litters (2 with 1 kitten each and 1 with 2 kittens) were present in winter 1972–73 as hare densities decreased to 200/100 ha. Hares were scarce again during winters 1973–74 and 1974–75 (69 and 34/100 ha, respectively), and no kittens were present, though 3 from at least 2 different litters were observed during 9–22 July 1973.

The occurrence of lynx kittens in winter populations therefore appears directly related to hare abundance. Litters were absent during 5 winters when hare densities were 137/100 ha and lower; mean litter size during winter increased from 1.3 to 3.5 as hare densities increased from 185 to 499/100 ha. Mean litter size at birth (3.9), as determined by placental scars of 102 female lynx collected in Alberta during 1972–75 (Brand and Keith, unpublished data), did not differ significantly between years or between areas of hare abundance and scarcity. Thus, our very limited information on numbers of kittens with adult females in winter suggests that partial survival of litters from birth to winter increased with hare densities.

We assessed reproductive changes in lynx by examining reproductive tracts of lynx carcasses supplied to us by trappers throughout Alberta. Preliminary results of these continuing investigations (Brand and Keith, unpublished data) suggested that changes in reproduction also may be a factor in the lack of kittens present during winter. Lynx are assumedly induced ovulators (Saunders 1961:46, Nava 1970:91), so the presence of corpora lutea can be used as an indication of conception. In regions of Alberta where hares were generally abundant during winter 1972–73, 76 percent of 41 yearling female lynx had corpora (had conceived) at 10 months of age; where hares were scarce, only 49 percent of 59 yearlings had corpora. There were no significant differences in adult conception rates or mean litter sizes between these areas. During a hare low in Newfoundland (1956–58), Saunders (1961:54) found that female lynx did not conceive until 23 months of age; however, during a hare peak and decline in Alaska, Nava (1970:94) reported that 53 percent of 566 yearling females apparently gave birth during their first year (as indicated by placental scars). He found the pregnancy rate of yearling lynx was lower, though, in an area of declining hare populations than where hares remained abundant for an additional year (83 vs. 92 percent, based on our calculations of Nava's data). There were no apparent differences in adult pregnancy rates.

It seems clear that lynx population declines are at least partly caused by a combination of greatly increased kitten mortality before winter and reduced rates of conception, especially among first-year females.

Home Range.—Because lynx populations at Rochester were resident over winter, and individuals apparently could be identified on the basis of predictability of movements and track distributions, we estimated home-range sizes during winter for individuals or family groups that were trailed more than 50 km. This estimate represented the minimum area covered by trails of known indi-

Table 2. Minimum home-range sizes of lynx and lynx families as determined by winter trailing on a 130-km² study area at Rochester, Alberta.[a] Home-range size was calculated for lynx that were trailed 50 km or more.

Winter	Period of trailing	No. days trailed	No. lynx	Distance trailed (km)	Minimum home-range size (km²)	No. lynx home ranges on study area	Hares/ 100 ha hare habitat[b] (1 Dec)
1965–66	21 Nov–24 Feb	34	1 adult[c]	98	18.7	5	79
1966–67	14 Jan –24 Mar	11	1 adult[c]	132	49.5	3	80
	11 Mar–30 Mar	19	1 adult	109	49.2		
1971–72	11 Jan –31 Mar	20	1 adult + 4 kittens	50	23.1		
	26 Dec– 8 Mar	15	1 adult	53	37.3	6	199
1972–73	6 Nov–15 Apr	23	1 adult + 1 kitten	70	12.4	6	200
1973–74	14 Nov–28 Feb	13	1 adult	72	11.1	5	69
	9 Jan –7 Mar	14	1 adult	72	23.3		

[a] Data for 1965–67 from Nellis et al. (1972).
[b] Hare habitat in the present paper is forest and brushland cover as discussed in text.
[c] This male lynx was trailed both in 1965–66 and 1966–67. Its track was identified by a missing toe.

viduals or family groups. The appropriateness of this method was reflected in the diminishing increment to home-range size with each additional kilometer trailed. In the present study, all estimates of home-range size continued to increase throughout the trailing period, and probably would have increased further with additional trailing; hence home ranges reported by us represent a minimum of the total area utilized during winter. Minimum home-range sizes in winter, calculated for 6 adult lynx and 2 family groups, varied from 11.1 to 49.5 km² and averaged 28.0 km² (Table 2).

Changes in home-range sizes of lynx might occur in response to changes in their own densities or those of their prey. There was no apparent relationship, however, between our minimum home-range size (Table 2) and either lynx or hare density (r = 0.28 and 0.01, respectively).

In Idaho, home areas of male mountain lions (*Felis concolor*) overlapped those of females but not of other males; female home areas often overlapped completely (Seidensticker et al. 1973). Mutual avoidance behavior keeps lions separated in both time and space, and territoriality (land tenure

system) appears to limit numbers of resident lions. In the present study, Nellis (Personal communication) noted that after a marked lynx was removed from the study area, a neighboring individual expanded its home range into the former's. Its tracks had never been seen there earlier. Some overlap of lynx home ranges, however, occurred in all years at Rochester. There was no apparent contact between lynx on home ranges that overlapped; areas of overlap were not used by different individuals at the same time. Because the sex of all single adults except one was unknown, we could not relate these home ranges to sex. Two females with kittens, however, tended to have a smaller average home-range size (17.8 km²) than did adults travelling alone (31.5 km²).

In Newfoundland, Saunders (1963b:395–397, 400) found that the home range of a female lynx with kittens (15.5 km²) overlapped that of a male (18.1 km²) and was also only slightly smaller than that of another male (20.7 km²) during the same winter. No other home ranges of resident males overlapped those of these two males,

though an apparent transient male was captured within the range of one.

From the above limited information it appears that some sort of social intolerance and mutual avoidance separates lynx in time and/or space, much as with the mountain lion. We could not determine if home-range overlap increased during periods of lynx abundance, but we suspect so since home-range size seemed unrelated to lynx densities. In Alberta during 1973–74, lynx catches by registered trappers indicated that high lynx densities occurred in isolated areas of hare abundance, and both hares and lynx were reported scarce in surrounding areas (Brand and Keith, unpublished data). In Newfoundland, Bergerud (1971) reported similar findings, suggesting that lynx may congregate in such pockets. From this it follows that the above-cited mutual avoidance behavior probably does not limit lynx densities locally.

Functional Response

Functional responses to fluctuating hare populations at Rochester have been documented for the great horned owl (*Bubo virginianus*) and the red-tailed hawk (*Buteo jamaicensis*) by McInvaille and Keith (1974). The relative biomass of hares in April–June diets of nestling horned owls increased from 23 percent during the hare low of 1966 to 81 percent during the high of 1971; the increase among nestling redtails during May–July was from 8 to 52 percent over these same years. Similarly, Todd and Keith (Unpublished data) recorded variations in occurrence of hares in the diet of the coyote (*Canis latrans*) in direct relation to changing hare densities. We wondered whether major dietary shifts also occurred among lynx at Rochester as hares fluctuated between scarcity and abundance.

Hunting Behavior.—Lynx used three hunting methods, all apparently well-suited for encountering and securing hares: (1) following well-used hare runways, (2) concentrating movements within small areas of hare activity, especially during hare lows, and (3) using short-term "waiting beds," depressions in snow that were not ice-encrusted, usually on ridges overlooking areas of hare activity or beside well-used hare runways.

Rates of encounters of lynx with hares were indexed as kill attempts/km of trail. Such encounter rates were directly related to hare abundance (Fig. 2); 91 percent of the variation in rates of attempted hare kills was attributable to changes in hare densities. Seventy-three percent of 361 kill attempts by lynx during this study were made on hares. The only other species of importance that lynx attempted to kill was ruffed grouse (15 percent of 361 kill attempts). Rates of encounters of lynx with ruffed grouse (Fig. 3) also were directly related
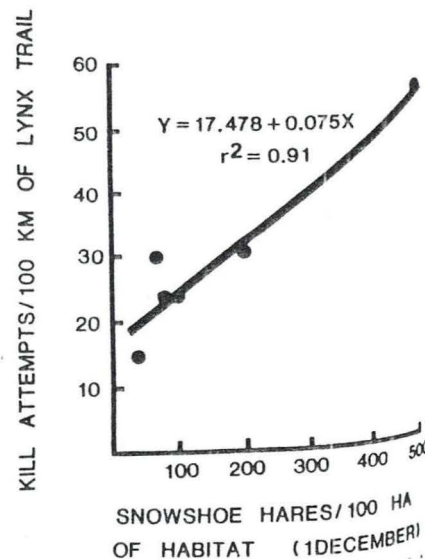
to grouse densities ($r^2 = 0.74$). These data suggest that the lynx is an opportunist, though lynx hunting behavior appears specialized for encountering hares.

Hunting Success Rates.—Because lynx depend upon hares as their staple food, during periods of hare scarcity they must increase their (1) hunting success rate (cap-

Table 3. Rates of successful capture of major prey species of lynx as determined by winter trailing at Rochester, Alberta.[a] Total number of kill attempts recorded in parentheses.

Prey species	Percent success						
	1965–66	1966–67	1971–72	1972–73	1973–74	1974–75	Weighted mean[b]
Snowshoe hare	24 (45)	9[c] (53)	24 (67)	34 (41)	21 (48)	36 (11)	23 (265)
Red squirrel	12 (8)	0 (5)	0 (1)	0 (6)	33 (3)	67 (3)	15 (26)
Ruffed grouse	19 (16)	8 (24)	(4)	50 (4)	33 (3)	67 (3)	19 (54)
Mean	22	9[d]	22	31	22	47	21

[a] Data for 1965–67 from Nellis and Keith (1968).
[b] Total successful attempts/total attempts × 100, calculated as follows: hare, 60/265 × 100; squirrel, 4/26 × 100; grouse, 10/54 × 100.
[c] Rate of successful capture of hares significantly lower in 1966–67 than in 1965–66 ($x^2 = 4.0$, $P < 0.05$).
[d] Rate of successful capture of all prey species significantly lower in 1966–67 than in all other years ($x^2 = 10.4$, $P < 0.005$).

tures/attempts), (2) use of alternative food sources, and/or (3) search effort (indexed here by distance travelled daily).

Rates of hunting success on hares were unrelated to hare densities. For example, the success rate of 9 percent in 1966–67 (Table 3) was significantly lower ($X^2 = 4.0$, $P < 0.05$) than that of 1965–66 (24 percent), though hare population levels were similar (Fig. 1). The 24 percent rate of hunting success in 1971–72, when hare densities were highest, did not differ from the 24 percent in 1965–66 or the 36 percent in 1974–75, when hares numbers were lowest. Hunting success on prey species other than hares showed the same trends, being lowest in 1966–67 and highest in 1974–75.

Apparent differences in capture rates of the lynx's 3 commonest prey were not statistically significant: hares, 23 percent; red squirrels (*Tamiasciurus hudsonicus*), 15 percent; and ruffed grouse, 19 percent (Table 3).

Foods.—Winter foods of the lynx during 1965–75, as determined from trailing and scats, were examined for functional responses to changing hare densities. Data on summer foods (from scats alone) were available during 1972 and 1973 only; we used these to examine responses by lynx to the increased number of potential prey

Fig. 2. Snowshoe hare densities in early December vs kill attempts at hares/km of trail by lynx during winter.
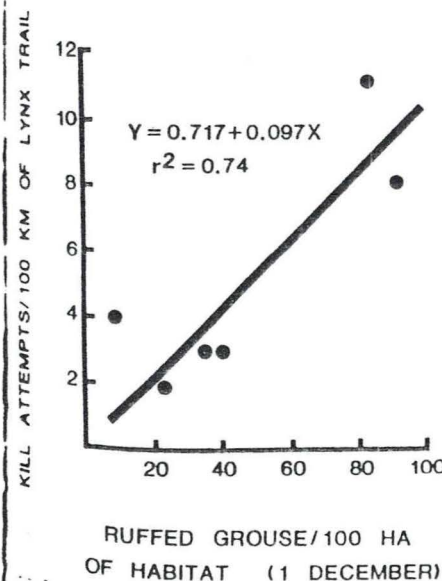
Fig. 3. Ruffed grouse densities in early December vs kill attempts at ruffed grouse/km of trail by lynx during winter.

Table 4. Number of occurrences and percent biomass of prey species and carrion in the winter diet of lynx as determined by trailing at Rochester, Alberta.[a] Snowshoe hare density (hares/100 ha) in December in parentheses.

Prey species	1965–66 (79)	1966–67 (80)	1971–72 (499)	1972–73 (200)	1973–74 (69)	1974–75 (34)	Total
Snowshoe hare	11/75[b]	5/43	16/100	14/90	10/96	4/81	60/82
Red and flying squirrel (Glaucomys volans)	1/ 1			1/ 1	1/ 1	2/ 6	5/ 1
Ruffed grouse	3/ 6	2/ 5		2/ 4	1/ 3	2/12	10/ 4
Miscellaneous[c]	3/ 3		1/tr		1/tr		5/ 1
Carrion[d]	2/14	6/52		1/ 5			9/12
Total	20	13	17	18	13	8	89

[a] Data for 1965–67 from Nellis and Keith (1968).
[b] No. occurrences/% biomass.
[c] One cinereous shrew (Sorex cinereus) was killed by lynx in 1973–74, two chickadees (Parus atricapillus and/or P. hudsonicus) in 1965–66, and one unidentified bird in 1971–72.
[d] Carrion use consisted of one domestic cat and one hare (1965–66); one hare, four visits to moose and one to domestic cow used as bait (1966–67); and one domestic chicken (1972–73).

Table 6. Distance travelled daily and daily kill and consumption rates of lynx as determined by winter trailing at Rochester.[a] Biomass of each prey item was adjusted to the actual amount of each carcass consumed. Biomass of carrion consumed at each meal was assumed to be one hare-equivalent. Number of bed-to-bed trails in parentheses.

Winter	Distance travelled daily (km)	No. kills/day		Biomass killed/day (g)		Adjusted biomass consumed/day (g)	
		Hare	Total	Hare	Total	Hare	Total
1965–66	4.7 (15)	0.4	0.5	550	560	450	540[b]
1966–67	8.8 (16)[c]	0.2	0.4	340	390	320	680[b]
1971–72	4.7 (10)	0.8	0.8	1,100	1,100	900	900
1972–73	3.0 (10)	0.7	0.7	960	960	960	960
1973–74	6.4 (13)	0.5	0.5	630	630	560	560

[a] Data from Nellis and Keith (1968) and Nellis et al. (1972) revised as discussed in text.
[b] Includes one visit to carrion in 1965–66 and four in 1966–67.
[c] Distance travelled daily was significantly greater during 1966–67 than during other years (P < 0.05, Duncan's new multiple-range test).

species (migratory birds and hibernating mammals) in summer.

Snowshoe hare was the most frequent item in the lynx's winter diet except during 1966–67. Trailing observations (Table 4) suggested that use of hares tended to be highest when hare densities were highest. Regression of percent frequency of hare in the lynx diet as determined by trailing against hare density indicated a significant but not strong functional response ($r^2 = 0.59$). This probably is to be expected with the low densities and/or availabilities of alternative prey species relative to the hare.

Trailing observations (Table 4) and scat contents (Table 5) indicated that about 40 to 75 percent of the prey biomass was snowshoe hare in 1965–67 and 1974–75, and essentially all was hare in 1971–74. Alternative food sources used in years of hare scarcity were primarily carrion, red squirrel, ruffed grouse, and small birds. In 1973–74, when hare densities were comparable to those of 1965–67 (Fig. 1), there was no use of carrion and less of a shift to alternative prey. We did not have annual indices to carrion availability, but during 1965–67 five of eight occurrences of carrion in the lynx diet represented visits to baits used to attract coyotes and lynx for livetrapping. We used no baits during 1971–75, and the nonutilization of carrion during these years probably represented a more normal situation on the study area.

Snowshoe hare appeared much less frequently (27 of 71 food items vs. 112 of 140) in scats collected during summer 1972 and 1973 than during the previous and following winters (Table 5). Mice and voles increased in occurrence from 22 of 140 items during the previous and following winter to 33 of 71 items during summer. Hares still comprised 91 percent of the total biomass consumed by lynx during summer, even with the increased prey base available. Saunders (1963a) also found an increase in the occurrence of birds and mice in the summer diet of lynx in Newfoundland, and van Zyll de Jong (1966) showed a similar decreased dependence on hares and increased variety of prey, especially microtines and birds, in the lynx's summer diet in Alberta.

Distance Travelled Daily.—The lynx is active from evening until early morning (Saunders 1963b). Trailing data suggested that most of these hours are spent searching for food. We used the distance travelled daily, i.e., the distance between consecutive daytime beds, as an indication of time and effort spent searching for prey.

The distance travelled daily by lynx might vary with two factors: changing hare densities and changing rates of hunting success. Multiple regression analysis of distance travelled daily on the above factors showed that the effect of hare densities was negligible; there was a significant negative correlation, however, between hunting success and distance travelled daily (partial correlation coefficient = 0.98). For example, lynx travelled an average of 4.7 km daily during 1965–66 (Table 6). During 1966–67 this increased to 8.8 km; hare densities were similarly low during these winters, but the hunting success rate decreased from 22 to 9 percent (Table 3). During 1971–72 lynx also travelled 4.7 km daily; the hunting success rate was identical to that in 1965–66, and hares were at their greatest density. The least distance travelled daily (3.0 km during 1972–73) occurred during the winter of greatest hunting success but moderate hare densities.

During the present study, lynx tended to concentrate hunting activities (and therefore largely movements) within areas of hare activity, especially during hare lows when habitat occupied by hares appeared restricted to areas of densest brushy cover

Table 5. Number of occurrences and percent biomass of prey species and carrion in the diet of lynx as determined from analysis of 260 winter scats and 38 summer scats.[a] Snowshoe hare density (hares/100 ha) in December in parentheses.

Prey species	November–April						May–October
	1964–67 (98)[b]	1971–72 (499)	1972–73 (200)	1973–74 (69)	1974–75 (34)	Total	1972 and 1973
Snowshoe hare	32/76[c]	31/99	46/95	35/97	15/94	159/91	27/91[d]
Mouse and vole	3/tr	7/tr	13/ 1	2/tr		25/tr	33/ 2
Red and flying squirrel	10/ 3			1/tr	2/ 2	13/ 2	1/tr
Ruffed grouse	9/ 6				2/ 4	11/ 2	
Miscellaneous[e]	4/ 1	1/tr	2/ 2		1/tr	8/tr	8/ 4
Carrion[f]	6/14		1/ 2	1/ 3		8/ 5	2/ 3
Total	64	39	62	39	20	224	71

[a] Data for 1964–67 from Nellis et al. (1972).
[b] Mean hare density for Dec 1964, 1965, and 1966.
[c] No. occurrences/% biomass.
[d] Relative occurrences of hare in the May–Oct diet of lynx significantly less than during previous and following winter ($X^2 = 36.9$, $P < 0.005$).
[e] Included 2 cinereous shrews, 1 porcupine (Erithizon dorsatum), 3 unidentified mammals, and 10 unidentified birds.
[f] Carrion utilization consisted of moose, white-tailed deer, and domestic cat, cow, and pig. Here we assumed each visit to carrion constituted one meal; biomass consumed was considered to be one hare-equivalent, as discussed in text.

(Keith 1966). Use of waiting beds (number of beds and time spent per bed) was not quantified, but if this method of hunting was more frequent at low hare densities it might explain why daily travelling distance did not increase during winters of hare scarcity.

Consumption Rates.—We have shown that rates of encounters by lynx with snowshoe hare and ruffed grouse, indicated by kill attempts/km of trail, were related directly to hare and grouse densities (Figs. 2, 3). Hunting success rates (kills/attempted kill) and search effort (distance travelled daily) were not related to hare densities. We therefore tested whether kill rates (kills/day) and consumption rates (biomass consumed daily/lynx) were related to hare densities. In 1965–66 and 1966–67 there were 0.5 and 0.4 kill daily/lynx (Table 6); included in these calculations were 10 hares, 1 red squirrel, and 2 ruffed grouse killed on 31 bed-to-bed trails. Adjusting for the actual amount of each carcass consumed by lynx, and adding estimates of carrion consumed during 5 visits to carrion on these trails, we calculated that each lynx consumed averages of 540 and 680 g/day, respectively, during these 2 winters.

The kill rate increased in 1971–72 and 1972–73 to 0.8 and 0.7, respectively (all were hares); the adjusted daily consumption rates were 900 and 960 g (Table 6). These were certainly maximum estimates during 1971–72 and 1972–73, for we assumed the entire carcasses of kills made by females with kittens were consumed by the adult female. Though Saunders (1963a) suggested that adult females hunt for their kittens until March, it seems likely that kittens would be developing hunting skills throughout the winter, being able to hunt entirely for themselves by spring. Indeed, of 17 kills made by female lynx travelling with

kittens during the present study, tracks of kittens were observed at only 7 of the kill sites; at the other 10 sites, the female consumed the entire carcass. If we divide prey biomass by the number of lynx (females plus kittens) present at kill sites, we estimate minimum consumption rates of 800 and 640 g daily for adults during 1971–72 and 1972–73, respectively. We do not know if, or to what extent, the mother shared her kills with her kittens when they were present at the kill site, but we suspect she fed herself first. Thus we believe the real consumption rate of adults is probably close to our estimates of maximum consumption.

In 1973–74, 6 hares and 1 red squirrel were killed (0.5 kill/day), and consumption averaged 560 g daily/lynx. Thus the average daily consumption rate/lynx during 1965–67 and 1973–74 (590 g), when hare densities were 80/100 ha of habitat and less, was 37 percent less than maximum rates during 1971–73 (930 g), when hare densities were greater than 130/100 ha.

Food requirements for lynx have not been well studied, but Saunders (1963a:390) reported that 2 captive adult lynx remained in "good condition" with an average consumption rate of 620 g/day. This value is similar to the mean daily consumption rate of 590 g/lynx during winters of hare scarcity in the present study—about 7 percent of the mean adult body weight (8.6 kg) of 10 lynx livetrapped between November and March at Rochester during 1964–68 (Nellis personal communication) and 1974–75. Golley et al. (1965:445) found that 2 captive adult bobcats (*Lynx rufus*) consumed 8.7 and 9.2 percent of their body weight daily in rabbits (*Sylvilagus floridanus*); 1 did not gain weight, and the other gained 6 percent of its initial weight in 25 days. We do not know the consumption rate at which lynx begin to lose weight, but we expect it is greater for lynx in the wild. Extrapolating

from food-requirement studies of dogs, Mech (1970:183) suggested that food requirements of wolves (*Canis lupus*) in the wild may be 25 percent greater than for "relatively nonactive" adult wolves in zoos. If this is true for the lynx also, the consumption rates observed during winters of hare scarcity in the present study may not have maintained lynx in "good condition," whereas the maximum consumption rate during winters of hare abundance (930 g, or about 11 percent of adult body weight) is indeed from 14 to 33 percent greater than the relative amount of food required to maintain lynx and bobcats in captivity.

CONCLUSION

A functional response by lynx to declining snowshoe hare densities reflected a shift in the occurrence of squirrels, ruffed grouse, and other birds, and increased use of carrion when it was available. The term "functional response" has been used commonly to connote such changes in prey occurrence in a predator's diet, but the real value to the predator of such a response is manifested in the accompanying change in relative prey biomass. For example, nearly seven red squirrels would be required to supply the food biomass of one hare; hence a drastic change in the frequency of occurrence from hare to red squirrel would be required to be nutritionally meaningful to a lynx. The biomass of one hare was at least twice that of any other prey species, so the functional response observed in the frequency of occurrence had little bearing on the actual percent biomass of hares in the lynx diet, with the exception of the marked increase in carrion representation during 1965–67.

The dietary shift from snowshoe hares to alternative prey and carrion during hare lows did not compensate completely for the low hare population, because a marked decrease in daily kill and consumption rates

was observed between winters of hare abundance and scarcity. We suspect the consumption rates during winters of hare scarcity in our study were perhaps about 20 percent below the normal maintenance level for a wild lynx. Such changes in consumption rates between hare highs and lows probably set the stage for numerical responses by lynx to changing hare densities.

Causes of postpartum mortality of kittens were thus most likely starvation related. Reduced kill rates during periods when a female lynx must hunt for and feed her young would affect nutrition of the kittens primarily, because the female most likely feeds herself first. Mortality factors for kittens are unknown, but may include outright starvation and/or sibling aggression during years of hare scarcity similar to that reported among arctic foxes (*Alopex lagopus*) by MacPherson (1969) during cyclic lows of lemmings (*Dicrostonyx torquatus* and *Lemmus sibiricus*). This also may explain the apparent partial survival of litters observed in the present study.

Those kittens that may have survived through winters of declining and low hare populations may have experienced nutritive stress that perhaps delayed sexual maturity (Sadleir 1969), thereby decreasing conception rates among yearling females, as suggested by our information from lynx reproductive tracts.

Starvation of lynx during hare lows of more pristine times has been noted (Seton 1911:96–98, Sheldon 1930:329), but outright starvation of adult lynx nowadays seems unlikely. Decreases in consumption rates probably first predispose them to other forms of starvation-related mortality; starvation may increase the likelihood of trapping lynx (Keith 1963:11) and/or increase lynx-human contacts in more settled areas where there may be more abundant

sources of alternative food such as carrion or domestic animals (Adams 1963).

Mutual avoidance behavior separating lynx in time and space did not appear to serve as a density-limiting mechanism during periods of hare scarcity of the present study, for lynx tended to concentrate in small local pockets of hare abundance during such times. The inability of the spacing mechanism to limit lynx densities effectively is similar to that reported among arctic foxes (MacPherson 1969), which also rely upon highly-fluctuating prey populations, but in contrast to the apparent density-limiting effect of territoriality among carnivores (notably the mountain lion and timber wolf) that rely upon relatively stationary prey populations (Hornocker 1970, Mech 1970:324).

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WHITE-TAILED DEER MIGRATION AND ITS ROLE IN WOLF PREDATION[1]

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Abstract: Seventeen white-tailed deer (Odocoileus virginianus) were radio-tagged in winter yards and tracked for up to 17 months each (881 locations) from January 1973 through August 1974 in the central Superior National Forest of NE Minnesota following a drastic decline in deer numbers. Ten wolves (Canis lupus) from 7 packs in the same area were radiotracked before and/or during the same period (703 locations). Deer had winter ranges averaging 26.4 ha. Spring migration took place from 26 March to 23 April and was related to loss of snow cover. Deer generally migrated ENE in straight-line distances of 0.0 to 38.0 km to summer ranges. Two fawns did not migrate. Arrival on summer ranges was between 9 April and 18 May, and summer ranges varied from 48.1 to 410.4 ha. Migration back to the same winter yards took place in early December, coincident with snow accumulation and low temperatures. Social grouping appeared strongest during migration and winter yarding. Survival of the radio-tagged deer was studied through 1 May 1975. Four deer were killed by wolves, one was poached, and one drowned. Mean age of the captured deer was 5.4 years and estimated minimum survival after capture was 2.6 years, giving an estimated total minimum survival of 8.0 years. This unusually high survival rate appeared to be related to the fact that both winter and summer ranges of these deer were situated along wolf-pack territory edges rather than in centers. In addition, most summer ranges of the radio-tagged deer were along major waterways where the deer could escape wolves.

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This study was prompted by a drastic decline in white-tailed deer killed by wolves in winter in the remote eastern half of the Boundary Waters Canoe Area (BWCA), in the Superior National Forest of northeastern Minnesota. Deer that traditionally wintered there had succumbed to a series of hard winters and wolf predation by 1971–72 (Mech, unpublished data). We hypothesized that since then, deer that occupied this region in summer migrated east to the Lake Superior Shore Deer Yard, or west to yards near Ely, some 96 km from Lake Superior.

To begin to test this hypothesis, and to learn some of the details of deer movements, we livetrapped deer in winter yards, fitted them with radio collars (Cochran and Lord 1963), and followed their seasonal movements. These winter yards were chosen because they were among the few locations where deer concentrations existed in the Ely area. We also used the deer data complemented by pack-territory data for wolves in the same area to gain insight into wolf predation on deer. The study was conducted from January 1973 to September 1974.

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IX. MANAGEMENT RECOMMENDATIONS

Human impacts to lynx populations in Washington are due primarily
to habitat changes and animal harvest. Historically,
impacts were minor and restricted to fringe or localized areas.
The climatic extremes of the environment coupled with low economic
resource values created minimal incentive to infringe on lynx
habitats. Impacts have changed as demands for timber and recreation
increase.

   A. Habitat

Early successional habitats are important for lynx in Washington and
are comprised primarily of dense stands of young lodgepole pine.
Similarly stocked stands were considered preferred conditions for lynx
in Montana (Koehler et al. 1979, Smith 1984). Winter tracking and
radio telemetry work in Nova Scotia (Parker 1981, Parker et al. 1983)
and Alaska (Stephenson 1984, Bailey et al. 1986) found lynx to select
for regenerating mixed forest types.

The importance of early successional forests to lynx is due to
a greater abundance of snowshoe hares in these areas. Conditions
which are good for snowshoe hares are good for lynx and the wildlife
manager must address the needs of both prey and predator.

A brushy understory, which provides both cover and winter food, is the

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common denominator of snowshoe hare habitat throughout their extensive geographic range in North America (Keith et al. 1984). The general trend in the seasonal food habits of hares is from woody browse, bark and needles during winter to more succulent herbacious vegetation in the summer (Wolff 1980, Bittner and Rongstad 1982). The amount of spruce and woody browse in the diet of hares in Alaska decreased from 82 percent of the diet in winter to 56 percent in April and to 25 percent in May (Wolff 1980). Clovers, grasses, sedges, ferns, and forbes are important foods for hares in summer (Aldous 1936). Thickets of densely stocked conifers or deciduous trees are seldom used in the summer because shade hampers undergrowth (Adams 1959).

In the fall woody vegetation begins to replace green plants as the primary food item for hares. Maximum use of woody vegetation occurs in winter when herbs and low shrubs are covered with snow. In deep snow, hares may reach vegetation as high as two meters (Dodds 1960). Winter diet is dependent on availability of plants (Pease et al. 1979); but an emphasis is often placed on conifers, willows and alders associated in dense thickets (Wolff 1980) where forage, hiding and thermal cover are in close proximity. Fox (1978) listed winter browse species in the order of preference and found willow, aspen, birch, hazel, and a number of other deciduous, second-growth woody plant species to be most preferred followed by white cedar, pines, firs and spruces. Prefered plants, too, often have greater nutritional value (Fox 1978).

Besides food, these dense thickets used by hares provide protective cover from avian and mammalian predators and shelter from the elements (Keith 1963, Wolff 1980, Pietz and Tester 1983). Heavy snowcover reduces the availability of protective cover near the ground. Tall shrub cover (greater than 1 m) is of greater importance than low shrub cover (0.5 to 1 m) because the low shrubs become buried during winter (Petz and Tester 1983).

These thickets are important to hares and during hare population declines act as reserves. As the population of snowshoe hares in Alaska declined, hares in marginal or suboptimal habitats were the most vulnerable and suffered the greatest loss (Wolff 1980). During

population lows, snowshoe hares are restricted to refugia of dense
cover (Keith 1963; Wolff 1980).

In Washington, densely stocked young stands of lodgepole pine provide
foods for hares in winter. They eat the tips of lodgepole pine
seedlings and lodgepole pine bark and find quick access to hiding and
thermal cover among the standing trees and downfall. Snowshoe hare
pellet transects on the Okanogan National Forest (D. Hays, pers.
comm. 1984) show substantially greater hare use in stands of densely
stocked lodgepole pine compared to old sparsely stocked stands.
Stocking rates ranged from more than 800 to less than 10 stems per
acre with the thicker stocked stands indicative of an earlier
successional stage. Once trees are of a certain size the actual age
of the lodgepole pine may not be as important as the bark
characteristics. Densely stocked stands retard tree growth and
maintain tightly barked trees which appear to be most attractive to
hares. Trees in the pole or small saw timber size class are less
frequently fed on by hares than are saplings.

Lodgepole pine dominates the early successional forest within the
lynx range in Washington because of relatively poor site conditions.
Where good soils or mesic conditions exist, willow and alder occur and

if densely stocked are frequently browsed by hares in winter.
Subalpine fir and Englemann spruce are found on less disturbed sites
but were seldom observed used as forage.

Modern forestry practices, however, change the habitat conditions for
snowshoe hare and lynx. Foresters have intensified management in once
remote areas because of increased economic values of timber and
concern over infestations of mountain pine beetle and spruce budworm.
This intensive forestry represents a two-edged sword (Nellis 1971)
with positive and negative attributes.

On the positive side, converting old growth forests and decadent
stands of lodgepole pine to early stages of plant succession will
benefit lynx by creating conditions favorable to hares.
Historically, these areas were maintained in an early successional
state by wildfires. Because of fire control and prevention, forests
have matured, reducing the carrying capacity for hares. Vegetation
within the reach of hares is in short supply in late successional or
climax forests but abundant soon after fire or logging (Fox 1978).

In addition to the benefits provided snowshoe hare, the conversion of
mature timber stands to early successional stages impacts other small
mammals (Tevis 1956, Svendsen 1981, Ramirez and Hornocker 1981,
Scrivner and Smith 1984). Small mammal populations are drastically
reduced immediately following clear cut operations. Thereafter,
select species increase to or above previous levels while others never
regain their former numbers until considerable regrowth has occurred
(Svendsen 1981). Overall, a net gain in small mammal numbers is
usually observed. Small mammals may be particularly important to
lynx when snowshoe hare numbers are low.

Forestry activities consistent with lynx management have the ability
to maintain, if not increase, lynx populations (Nellis 1971, Burris
1971, Parker et al. 1983). Timber harvest managed under a long term
sustained yield philosophy can provide for a needed change of forest
conditions, and less dramatic than massive wildfire.

However, clear cutting, the most common method of timber harvest, has
the potential to eliminate cover over large areas. In the past
these areas have exceeded several hundred acres. More recently,
particularly with multiple use public agencies, clear cut size has
been reduced but may still exceed 100 acres. The short-term impact of
this removal is uncertain (Parker et al. 1983), but it does eliminate
habitat for snowshoe hare and lynx until satisfactory vegetation
returns . Keith and Surrendi (1971) noted that hares reoccupied
severely burned areas within 15 months. The recovery of sufficient

cover for lynx may take longer, perhaps up to 15 years or more In
fragile, high elevation ecosystems. Lynx avoid crossing large
openings created by clear cutting, selective logging or extensive
thinning. Openings created by logging Is considered to be an
Important factor In discouraging use by cougar In timber sale areas of
Utah (Van Dyke et al. 1986).

Logging roads and Increased vehicular traffic and human activity may
adversely effect lynx as It does for cougar (Van Dyke et al. 1986).
Impacts from roading Involves direct loss of habitat, Indirect loss of
habitat by avoidance of human activity areas, greater accessibility to
the legal trapper or hunter, and greater vulnerability to poaching.
Impacts from traffic Include snowmobile use In winter. Although
travel and harvest restrictions can regulate legal harvest,
opportunities for the Illegal take of lynx will Increase.

Elimination of mature subalpine fir and Engelmann spruce stands also
may Impact lynx. Although not as valuable throughout the year to lynx
as early successional conditions, they are an Important ecological
component of lynx habitat, especially during Inclement winter weather,
drought, or denning periods. Denning Information suggests lynx use
upturned spruce roots, hollow logs, refuges under windfalls, and
beneath conifer boughs as denning sites (Berrie 1973; Gugglsberg
1975). Similar refuges may be Important to lynx during Inclement
weather. Bailey (1974) and McCord (1974) noted the Importance of
certain refuge sites to bobcats during severe weather.

Forestry practices often leave little if any large debris on the forest floor. Slash is removed, compacted, or burned to encourage regrowth of trees or to minimize "fuel loading" for fire prevention. The remaining small diameter limbs are easily compressed by winter snows and deteriorate over a relatively short period of time. Natural conditions provide for numerous large diameter fallen snags in young forests or in more mature stands, an assortment of fallen poles. Consequently, an important component of hiding and thermal cover for hares and stalking cover for lynx is lost.

Forestry practices often encourage the more economically desireable trees such as subalpine fir, Douglas fir, Engelmann spruce, larch, and Ponderosa pine at the expense of lodgepole pine. These species are often planted following timber harvest or encouraged through selective logging and thinning practices. As the dominant tree types change so too does the ecosystem.

c.) at least 100 tree stems per acre.

Stem density may be reduced if significant down material or
bushy trees are present.

Forage/Hiding/Thermal-Stalking Cover is most often associated with
early successional stage forests. Here suitable winter forage in
close proximity to hiding and thermal cover is available to snowshoe
hares. Hiding cover is necessary to escape both avian and terrestrial
predators, and thermal cover reduces energy expenditure during cold
temperatures. The dense understory of these types enables lynx to
stalk and capture snowshoe hares.

Key characteristics are:

a.) both deciduous shrubs and trees or coniferous trees;

b.) coniferous stands are at least 75 percent lodgepole pine;

c.) trees and shrubs are at least six feet tall providing cover for
snowshoe hares and lynx during heavy winter snows, which may
cover vegetation shorter than six feet;

d.) densely stocked stands of sapling trees;

e.) down material, a key component, provides cover and is most

Important where cover is not brushy or during heavy snowfall

and

f.) contiguous with travel cover.

Vegetative Manipulation

1.) Lynx habitat management guidelines should be applied to all
forest ecosytems wherever lynx occur in Washington, particularly
the primary zone (Figure 3.23). Although lodgepole pine plant
communities are important, other communities must be managed as
well.

2.) Forestry practices should provide a plant community mosaic of
early successional forests with a diversity of trees and shrub
species, age classes, and life forms. These successional stages
should be distributed over time and space.

3.) Managed stands should not exceed 40 acres in size.

4.) Forest management may include timber harvesting and
thinning or fire management depending upon site specific goals.

5.) A balance of stand types must be maintained, facilitating a
sustained yield of natural resources over time. For lodgepole
pine dominated stands this would be represented by an equal
amount of grass-forb-shrub seedling, sapling, and pole-small saw
timber cover types.

6.) Cover ratios should be based on a 640 acre management unit
with vegetative ratios prescribed in Table 3.7.

Table 3.7. Recommended cover ratios for lynx habitat in managed
forests of Washington.

	Primary Zone
Denning Cover	6%
Travel Cover*	30%
Forage/Hiding/Thermal- Stalking Cover**	30%
Non-Lynx Cover Areas***	33%

* primarily includes pole-small saw timber stand categories.

** primarily includes sapling stand categories.

*** includes grass-forb-shrub-seedling stand categories <u>and</u>
natural openings (water not included).

7.) Lynx avoid large openings, therefore natural and man-made openings should never exceed 33 percent of the land.

8.) Down material and other woody debris should be left following timber harvest to provide forage/hiding/thermal-stalking cover. Logs left after fire or clearcutting provide cover during forest regeneration enabling wildlife to more rapidly utilize new forage areas.

9.) Lodgepole pine must be maintained and not converted to more economically valuable tree species.

10.) Forestry practices should be closely monitored to evaluate their impact on lynx and snowshoe hare habitat. Timber thinning will increase non-lynx cover areas.

11.) Application of herbicides, if considered necessary, must occur at a time when there will be little adverse impact on browse for hare. It should be a species specific herbicide as well.

12.) Cattle grazing should be monitored to minimize impacts to snowshoe hare habitats. Grazing by cattle may compete with hare use of deciduous brush or trees, such as along riparian areas.

13.) Clearcuts should be limited to 20-40 acres in size.

Openings are avoided by lynx, but the edges created by harvesting may benefit hares. The width of openings should not exceed a width of 1200 feet, less than 600 feet width would be optimal.

14.) Major ridges should be managed for travel cover, with special emphasis on saddles. Travel cover corridors must be greater than 300 feet wide. Managed stands should be designed to provide parallel corridors so as not to break up travel cover corridors.

15.) Trees in harvested units should be six feet or taller, before adjacent areas are harvested or thinned.

16.) Snowshoe hare numbers should not be controlled. Harvest seasons on snowshoe hares should reflect the value that hares play in the ecosystem occupied by lynx and other boreal predators.

1.) Minimize road construction, particularly main access roads.

2.) Construct and maintain roads to minimum possible standards to discourage heavy use; the more primitive, the better.

3.) Destroy roads following logging operations. Gates, ditches and other obstacles may discourage access in summer but planting trees in the roadbed may be more effective to discourage snowmobile use. Specific areas may be closed to access to protect down material from firewood cutters and to aid law enforcement efforts.

4.) Construct deadend roads rather than loop roads to minimize public use disturbance.

Lynx seasons in Washington need to be conservative because of the
animal's low numbers, limited distribution, restricted environments,
years with little or no reproduction, habitat loss, increased
accessibility, and high demand by sportsmen for lynx pelts.
Seasons in the past, particularly during the early 1970's in the
Kettle Range (Ferry County), may have been detrimental to local
populations.

In the past, Washington lynx populations have benefitted from cyclic
population highs in Canada. Harvest in Canada has impacted
populations there which affects the influx of lynx into Washington.
Consequently, Washington may no longer receive a boost in recruitment
as large as those during previous times.

Seasons could follow an approach described by Brand and Keith (1979)
where harvest is curtailed for three to four years during population
lows. Unfortunately detecting the population cycles in Washington is
difficult, due to the low harvest numbers, without considerable
investment of time and money. Snowshoe hares are likewise difficult
to monitor and currently not monitored in the state. Relying on
British Columbia trends would be a possibility, but risky, due to
regional variations in cycles. Consequently, a strategy which allows
for a static harvest level acceptable even during population lows
would be overly conservative during high periods but not jeopardize

lynx during low times.

Permits appear to be the most viable option of continued harvest.
Permits should apply to all harvest, both trapped and hunted. A
permit system allows for quotas to be set and actual harvest
distributed over available habitats. It also prevents excessive
harvests. Season dates can be variable since harvest rates would be
regulated by permits rather than season length.

Once a permit system is established, it becomes a political question
of who gets to harvest lynx. Trappers, houndmen, predator callers and
a variety of sportsmen have shown an interest in lynx and may be
illegible for a permit. Permits should be distributed by drawing with
successful applicants having to wait two years or more before
reapplying.

Within ten days of killing a lynx, the hide should be presented to a
State Wildlife Agent or a Department office for tagging. All lynx
carcasses should be submitted to the Department for examination. A
follow up questionnaire including information about hunting effort and
tracks observed should be conducted following the season closure.

Observations on Home Range Sizes, Movements and Social Organization of Lynx, *Lynx canadensis*, in Riding Mountain National Park, Manitoba

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Of a total of five Lynx (*Lynx canadensis*) captured, three were radio-collared and their movements studied. All radio-collared Lynx were later killed by trappers adjacent to the park. Home ranges for two females averaged 156 km² and that of a single male was 221 km². These figures are higher than reported in the literature. Two females travelled with their kittens together for a short interval. Riding Mountain National Park does not appear to be large enough to sustain a viable Lynx population over time, and reinvasion of Lynx from outside areas may be necessary to maintain populations.

Key Words: *Lynx canadensis*, Lynx, home range sizes, movements, Riding Mountain National Park.

Although widely distributed in Canada and important as a commercial fur animal, the social behaviour of Lynx has not been extensively studied. Several studies have centred on food habits (Van Zyll de Jong 1966; Nellis and Keith 1968; Bergerud 1971; Nellis et al. 1972; Brand et al. 1976; Parker 1980).

Data on home ranges and movements have been obtained from trapping and recaptures (Saunders 1963), snowtracking (Brand et al. 1973) and radio-tracking (Berry 1973; Koehler et al. 1979; Mech 1980; Parker, in preparation). Mech (1980) compared the methods and concluded that radio-tracking overcomes difficulties inherent in the other methods.

This paper describes the movements of Lynx captured and radio-collared in Riding Mountain National Park. Data were collected secondarily to other large carnivore studies on wolves and coyotes.

Description of Study Area

Riding Mountain National Park, 2944 km² in size, is located in southwestern Manitoba (Figure 1), approximately 200 km northwest of Winnipeg. The Park is surrounded by agricultural lands and as such forms an isolated wilderness system.

Bailey (1967) described 12 main cover types within four vegetational associations. These associations are grassland areas, interspersed through the western portion of the park, two subcomponents of the boreal forest and northern elements of deciduous forests (Rowe 1972). Predominant vegetation are aspen (*Populus tremuloides*) and mixed forest stands. Relief, drainage and fire history govern plant cover in localized areas. Within historical times, haying, cattle grazing and logging contributed to human-induced changes, however such activities have ceased in recent years.

Interspersed throughout the park are numerous ponds, lakes and a few streams. In the northern and eastern portions of the park the plains are deeply incised by streams flowing across an escarpment along the eastern portion of the park. Westward the terrain blends into the prairies and forms a plateau with a series of gently undulating hills.

Methods

Lynx were captured in No. 4 or No. 14 leg hold traps incidental to capture programs for Wolf (*Canis lupus*) and Coyote (*Canis latrans*). Trapped Lynx were anesthetized with equal porportions of phencyclidine hydrochloride and promazine hydrochloride at dosages of 1 mg of each drug per kg of Lynx weight. Captured Lynx were measured, weighed, ear-tagged, radio-collared and then released. Radio fix locations were monitored with a Maul M5 aircraft and plotted on topographical maps. Home range sizes and distances between fixes were calculated using a Hewlitt Packard 9830 desk computer. Fixes were sequentially numbered to detect whether spread of locations reflected movements within a home range or dispersal to new areas. Efforts were made at each relocation to see the animals and record group sizes of females with kittens. All radio fixes of the females were from the winter (November–April) period and only 4 of the 49 fixes of the male were from the August-October period, the remainder covered the winter period.

Results

Five Lynx were captured and three of these were radio-collared. Two animals from different family groups and a lone animal were radio-collared (Table 1). Radio-marked Lynx were studied over periods ranging from 86 to 228 days, and in one case recovery
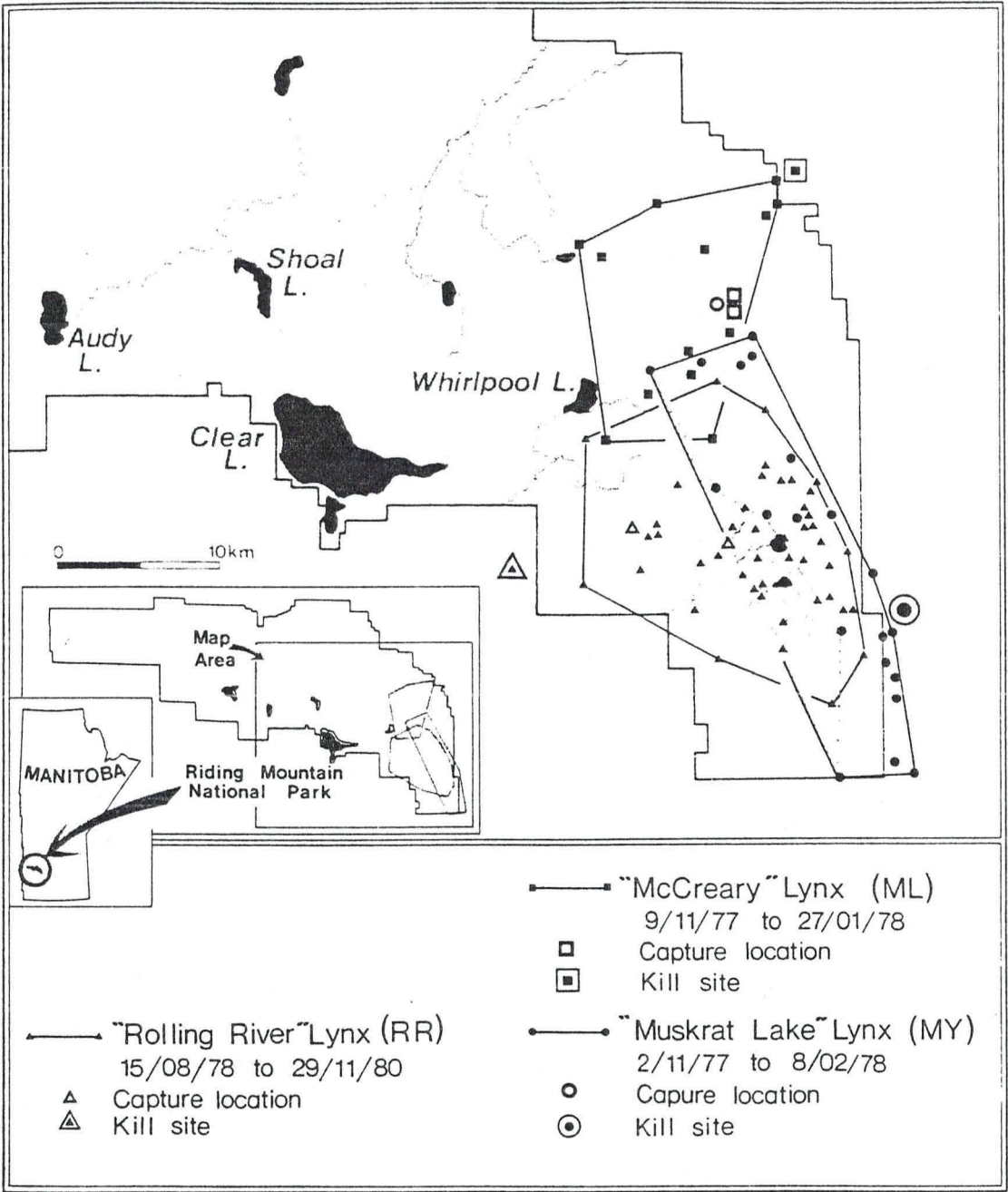
FIGURE 1. Home range delineations of radio-collared Lynx studied in Riding Mountain National Park, Manitoba.

TABLE 1. Monitoring frequency, social status, movements, and home ranges of Lynx radio-collared in Riding Mountain National Park

Sex	Age	Social status	Weight (kg)	Capture date	No. of fixes	Monitoring Frequency (days)		Distances between fixes (km)		Sample Size	Home range km²	Fate
						Total period $\bar{x} \pm$ S.D.	Intervals 3 days $\bar{x} \pm$ S.D.	Total $\bar{x} \pm$ S.D.	3 day intervals $\bar{x} \pm$ S.D.			
Female MY	Adult	Travelling with two kittens when captured	13.6	9-11-77	14	5.5 ± 7.8	2.4 ± 0.7	5.6 km ± 3.5	4.8 km ± 2.9	n = 8	138	Female and one kitten trapped 27-1-78; fate of 1 kitten unknown.
Female ML	Adult	Travelling[1] with two kittens when captured	10.9	2-11-77	22	4.6 ± 6.3	2.4 ± 0.7	4.3 km ± 3.0	3.1 km ± 1.9	n = 13	177 (118)[3]	Female trapped 8-02-78; fate of three kittens and second adult unknown.
Male RR	Adult	Travelling alone	15	15-8-78[2]	49	4.7 ± 8.3	1.6 ± 0.7	4.8 km ± 3.8	3.8 km ± 2.2	n = 34	221	Monitoring stopped 31-03-79. Animal trapped 29-11-80.

[1]This family group was joined on 9 January 1978 by a second adult with kitten. The group of five Lynx travelled together until 8 February 1978 when the collared Lynx in the group was captured.
[2]First captured (but not collared) 22 September 1976.
[3]Adjusted to include inside points only (see Figure 1).

of a Lynx occurred 836 days after capture (Table 1).

An adult female (ML) weighing 10.9 kg was captured on 2 November 1977. There was no evidence that the female was still nursing her young. This animal travelled with two kittens, and based on 14 radio fixes covered an area of 138 km² (Figure 1). These three animals were joined by two others (noncollared) which from aerial observations appeared to be a female with kitten. On five different occasions, spanning a period of 30 days (9 January to 8 February) these five animals were seen travelling together. The radio-collared female was killed by a trapper outside the park on 8 February 1978.

Another adult female (MY) was captured 9 November 1977 and weighed 13.6 kg. A kitten, travelling with her and weighing 8.2 kg was captured at the same time. Home range, based on 22 fixes, covered by these two Lynx was 177 km² in size (Figure 1). Based on inside points only (see exclusion of shaded area) the home range was 118 km². A trapper killed the animal 27 January 1978.

An adult male (RR) weighing 15 kg was captured and radio-collared 15 August 1978. This animal had been previously trapped and ear tagged on 22 September 1976, but was not radio-collared at that time. This Lynx was killed by a trapper adjacent to the park 29 November, 1980. Home range (15 August 1978 to 29 November 1980) of this male was 221 km² (Figure 1).

Locations of radio fixes were plotted (Figure 1) and the time intervals listed (Table 1). Mean distance between fixes for adult females were 5.6 km and 4.7 km respectively and 4.8 km for the male. Since time intervals between monitoring dates were often widely spaced apart the distances for winter months were recalculated to include fixes which were obtained within three day intervals. Average distances between fixes in three day periods were 4.8 km, 3.1 km and 3.8 km for the two females with kittens and for the male respectively. Actual distances travelled probably were considerably longer.

Discussion

The status of Lynx populations in the past within Riding Mountain National Park has been uncertain. The species was not listed by Green (1932). Soper (1953) believed that only a few individuals migrate from time to time into the park. Soper did not see much evidence of the species while conducting field work in the 1940's. Other previous records indicate the often sporadic abundance of the species.

During the duration of this study Lynx were reported only for the eastern portion of the park. Intensive winter field work was carried out in the western portion on wolf/ungulate studies and on Showshoe Hare (*Lepus americanus*) (Leonard 1979,

Poll 1981, Parks Canada and C.W.S. unpublished reports). Observers failed to see any sign of Lynx at that time. Since then wardens (A. Cochrane, personal communication) have seen a few Lynx in the winter 1980/81 in the western portion of the park. Concentration of Lynx in localized pockets were also found in Newfoundland (Bergerud 1971), Alberta (Brand et al. 1976) and Minnesota (Mech 1980). One trapper around the park reported trapping 16 Lynx in a restricted area (about 3 km²) over a short period of time (January, early February) in 1982 (P. Paquet, personal communication). From observations elsewhere in Manitoba it appears that the provincial Lynx harvest peaked in 1978/79 and since then numbers have declined (R. Stardom, personal communication). Harvest statistics have revealed that the peaks begin in the northwestern portion of the province and move progressively outward from that focus. The peak in Lynx pelt production in the western part of the province, including the RMNP area, occur 4-5 years after the harvest has peaked in the Pukatawagun/Nelson House area. The province-wide peak in pelt production appears to occur when Lynx numbers are high over the greatest area. This study was conducted at a time when Snowshoe Hare numbers were at or near peak levels in the eastern portion of the province and Lynx in the park could have dispersed from more northerly areas. The Snowshoe Hare population in the park previously peaked in 1970/71 and was rapidly increasing by 1978 (Poll 1981, unpublished CWS report). In the early to mid 1970's Lynx were seen on several occasions by L. Carbyn and G. Trottier in the central portion of the park. Warden observations for that period suggest only sporadic distribution of Lynx (Kingsley and Stelfox 1978, CWS unpublished report). Fur returns for the province of Manitoba indicated record high Lynx catches for 1971 (R. Stardom, personal communication). South of Manitoba Lynx began appearing in Minnesota in 1972 (Mech 1980) which probably dispersed from the north.

The general absence of large numbers of Lynx in the early 1970's and increase at a time when the Snowshoe Hare cycle was increasing could explain why the home range sizes reported here are larger than any reported to date in the literature. Previously the largest home range sizes for female Lynx ranged from 51-122 km² (Mech 1980). Female Lynx home ranges in Riding Mountain were 156 km² and unlike Minnesota Lynx, the females in this study were travelling with kittens. These figures are based on comparable methods in home range delineation as described by Mech (1980). If only the inside points of the home range perimeter (see Figure 1) are used in the aerial calculations then average female home range sizes would be 128 km².

Calculation of territory size and home ranges for carnivores requires more detailed attention. In Wolf studies within the Park (Carbyn 1980, unpublished CWS report) a large number of fixes in relatively small territories were plotted at five fix intervals to determine asymptotes at which upper limits of territories were defined. This approach probably is less applicable to social units or individuals with large home ranges. However, since only small numbers of radio fixes were available for Lynx in this study, it is likely that the larger territory sizes, using outside points only, are more representative of true home range sizes. The home range of the single male (221 km²) was similar to the range reported for Minnesota. Extensive radio-tracking in saturated Lynx populations in Nova Scotia resulted in much smaller territory sizes (G. Parker, personal communication).

Mech (1980) suggested that spatial organization of Lynx in Minnesota was similar to that of Mountain Lions, *Felis concolor*, (Seidensticker et al. 1973) but differed from Bobcat (*Felis rufus*) (Bailey 1974). That is, female Lynx ranges tend to overlap both spatially and temporally, whereas male ranges to not overlap with other males or with females. In this study both females with kittens were caught at the same locations and ranges overlapped. The range of RR male Lynx overlapped with the territory of ML female, but this could have been as a result of the loss of ML female from her range, since monitoring of the male's movements occurred after the female's death. Our data therefore are inconclusive as to whether male/female ranges were separated, although results do imply this to be the case.

Radio-tracking of Lynx indicated that the park population is vulnerable to outside non-park oriented activities. All five captured Lynx, including the three radio-collared animals, were killed by trappers. High human-induced Lynx mortality was also reported in the radio-collared Lynx in Minnesota (Mech 1980). We believe that in years of low Lynx numbers and high trapping pressures it is possible that the entire population in the park could become extirpated and numbers may then have to be replenished from movements by Lynx from other areas. Under present conditions, therefore, it does appear that the park may not be large enough to sustain a viable Lynx population over time, when a combination of factors such as high trapping pressures around the periphery of the park and low hare densities coincide and persist for a number of years. Further research would be required for clarification.

Degree of dependence of kittens on their mother is important in setting harvest regulations. In this study kittens travelled with adult females well into midwinter. Judging from teat size it is improbable that young

were still nursing. It was not possible to determine when kittens begin to establish their own home ranges or become separated from the parent. Trappers in northern Alberta recognize the vulnerability of family groups to trapping and take advantage of it by setting several traps in specific areas. Cases have been reported where only adult females were caught and kittens froze to death at the side of the dead parent (P. Galbraith, personal communication). Parker (1980) stated "hunting success must be an important learned behaviour by kittens during their first year of life. The extent of mortality among kittens, whose mother is trapped early in winter is completely unknown." Our observations agree that this could be an important factor in management of the species. The fact that we observed two adult females travelling with their kittens, would suggest that under some circumstances the loss of one female may lead to the adoption of the surviving kittens by other adults in the group. Because of the economic importance of this species, we urge further research on its social behaviour for better understanding of life history as a basis for effective management.

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A lynx kitten bats its mother's ears. Lynx populations require close monitoring because the cat's fur is popular in the fashion industry. *Photo Researchers*

The Lynx

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SPECIES DESCRIPTION AND NATURAL HISTORY

The lynx (*Felis lynx*) is a predator of the Northern Hemisphere's high-latitude and deep-snow boreal forest ecosystem. Traditionally, North American and Eurasian lynx were considered different species, *Lynx canadensis* and *L. lynx*, respectively. However, many authorities now believe the two are subspecies. A third population, the Spanish lynx of the Iberian Peninsula, is considered a separate species, *Felis pardina*, by some and a subspecies, *F. lynx pardina*, by others. Taxonomic and evolutionary relationships still are not clear (Corbet 1978, Nowak and Paradiso 1983).

Physical Characteristics

In North America, lynx measure from two to three and a half feet long and weigh 10 to 40 pounds (Banfield 1974, Saunders 1964). Eurasian lynx are somewhat larger, measuring up to four feet long and weighing up to 70 pounds (Novikov 1962). Males generally are larger than females, and weights and physical dimensions also vary geographically (McCord and Cardoza 1982).

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Coloration varies from yellowish brown to gray, often with a pattern of dark spots. The short tail may have several dark rings and is tipped with black. Long, ruff-like fur on the lower cheeks and tufts of black hairs on the tips of the ears give the lynx a distinctive face. The legs are relatively long and the paws large and densely furred, an adaptation for moving over snow.

Although similar to the bobcat (*F. rufus*), the lynx can be distinguished by its longer legs, larger feet, and longer ear tufts. It lacks the bobcat's more definite markings over the body, and its tail is black-tipped above and below, while the stubby tail of the bobcat is black only on the upperside of the tip (Murie 1963).

Lynx generally are noctural or crepuscular. Highly resistant to cold, they appear to be affected adversely by hot weather. They have poor endurance and usually ambush rather than chase prey (Banfield 1974).

Range

Lynx are found throughout Canada except for the northern regions of Labrador, Quebec, and the Northwest Territories; the arctic archipelago; and the coastal mountains of British Columbia (McCord and Cardoza 1982). They inhabit most of Alaska, except for the coastal regions, but in the contiguous United States the only substantial populations are in northern Washington and Idaho and northwestern Montana, with lower densities extending down the Rocky Mountains into Utah and Colorado (McCord and Cardoza 1982). A few live in northern New England. On occasion, especially during periods of high population levels in Canada, lynx are found in the states of the northern plains and upper Great Lakes (Adams 1963). Lynx densities throughout the range vary widely, with highs and lows occurring in the 10-year population cycle. Density estimates are not available for most areas, but in Alberta lynx numbers changed from 10 to two individuals per 40 square miles during a decline in the snowshoe hare (*Lepus americanus*) population (Brand and Keith 1979).

Lynx also are widely distributed in the forest zone of the Soviet Union, the mountains of central Asia, and throughout western mainland Europe (Novikov 1962). The endangered Spanish lynx formerly occurred throughout the Iberian Peninsula, but now is restricted to scattered mountainous areas and the Guadalquivir Delta (Nowak and Paradiso 1983).

Lynx habitat has been described generally as climax boreal forest with a dense undercover of thickets and windfalls. Advanced successional stages of forests and dense conifer stands often are selected as habitat (Banfield 1974). Habitat quality and food abundance can influence home range size, which normally averages from four to 20 square miles per individual and at times up to 80 square miles (Brand *et al.* 1976, Carbyn and Patriquin 1983, Saunders 1963). Lynx reportedly move three to 18 miles a day. A movement of almost 300 miles was recorded for a young female (Mech 1977).

Reproduction

Mating occurs mainly in February and March, beginning about mid-February in more northerly regions. Females bear a single litter of one to six, usually two or three, young yearly (Saunders 1963). Gestation lasts nine or 10 weeks, and kittens are born mid-May to mid-June.

Lactation can last for five to six months, but some meat is eaten by two- to six-week-old kittens. The young usually remain with their mother until the winter mating season, and siblings may stay together for a while afterward (Nowak and Paradiso 1983).

Diet

Lynx throughout North America and Europe show remarkable consistency in diet. Little doubt exists that this cat is especially adapted to prey on rabbits. The snowshoe hare is the major prey species in North America, the mountain hare (*L. timidus*) is a primary food source in Europe, and the Old World rabbit (*Oryctolagus cuniculus*) is the basic prey of the Spanish lynx. Hares can comprise some 80 percent of the lynx diet. It has been estimated that lynx make a kill every other day and that an individual lynx may eat 170 to 200 hares yearly, plus a few birds and mice. Lynx sometimes cache prey and return later to feed upon them (Saunders 1963).

Grouse, squirrels, and small rodents can be important alternate prey items for all lynx populations. Ungulates in northern Europe and the Soviet Union and ducks on the Iberian Peninsula often make up a large portion of the diet (Borg 1962, Delibes 1980).

In North America, lynx rely on snowshoe hares more during winter than during summer. Their diet varies more when there is no snow cover, probably because of the greater availability of small mammals. However, snowshoe hares still comprise the majority of prey consumed during summer months. In some parts of Europe, lynx change their diet in early winter from one of hares, small mammals, and birds toward a higher proportion of ungulates (Birkeland and Myrberget 1980). Snow conditions can greatly influence hunting success. When the weight-bearing strength of snow is low, lynx will break through, while hare and grouse prey do not (Nellis and Keith 1968). Soft, deep snow also hinders the hunting ability of lynx. Thus in certain years with poor snow conditions, success can be low even if prey densities are high.

Population Cycles

North American lynx population trends probably have been recorded longer than those of any other wildlife species. Fur returns, useful as an index to population growth and decline, were recorded by the Hudson Bay Company for more than two centuries. Several authors have pointed out that fur returns, indicative of the size of the lynx population, fluctuated regularly from extremely high levels to very low levels, about every 10 years. The periods between peaks in population levels vary somewhat, but less than would be expected by chance (Bulmer 1974).

One researcher described the 10-year cycle as follows, "the basic cause of the cycles is the [snowshoe hare] interacting with its vegetable food to produce a predator-prey oscillation. When the rodents decline in numbers, the [lynx] become short of food, prey upon and cause the decrease of the gallinaceous birds of the same region and themselves die of starvation and/or emigrate . . . in large numbers [which] helps to synchronize various regions" (Lack 1954).

The following points about the 10-year cycle also have been made: (1) lynx have followed a 10-year cycle at the continental level for the past 200 years, (2) lynx can remain common in some areas two to three years after the hares decline, though in Alaska, lynx declined immediately after hares declined, (3) lynx fluctuations have been more extreme than those of other furbearers, (4) mass movements of hares, lynx, foxes (*Vulpes vulpes*), martens (*Martes americana*), and other species probably have taken place, and (5) the amplitude of recent lynx cycles has declined markedly as the peaks in the cycle have become lower (Bailey *et al.* 1986, Keith 1963, O'Conner 1984).

SIGNIFICANCE OF THE SPECIES

The lynx has important economic, recreational, scientific, and aesthetic value. Throughout its range it is classified as a furbearer and provides recreational opportunities and economic returns for trappers. More recently, formal seasons have been established in the northwestern United States for hunters who use hounds to pursue and tree lynx. Pelt values can vary considerably with individual quality and demand, but generally provide some of the highest monetary returns of any fur.

In certain instances, lynx may regulate or influence some prey population levels. Declines of arctic hare (*L. arcticus*) and caribou (*Rangifer tarandus*) on Newfoundland have been attributed to lynx predation pressure (Bergerud 1967, 1971). However, it is generally believed that lynx do not cause the density of their rabbit prey to

decline, but rather the level of available prey influences the surviv abundance, and reproductive success of the lynx. Nevertheless, w hare numbers are low, lynx may keep the hare population depresse two or three years before the increase phase begins.

In some high-elevation forests in the Pacific Northwest presence of the lynx is considered an indicator of ecosystem integ In these areas, lynx generally inhabit the timbered ridgetops and sl where harvests of such species as lodgepole pine (*Pinus contorta* being planned.

The scientific value of the lynx is tremendous. The 10-year c is among the most intriguing phenomena in nature. Much cai learned about predator-prey relationships, wildlife population dyn ics, and the ecology of predators in general and felids in particular f the study of the lynx. Aesthetic values are nebulous and impossib quantify realistically, but to many people the lynx's secretive nai periodic abundance and scarcity, and ability to survive in severe wi cold and deep snow make it a symbol of the boreal forest.

HISTORICAL PERSPECTIVE

The range of the lynx in North America before European settler probably was very similar to what it is today, with the exception c southern edge. It is possible that lynx range once extended sout cover the northern third of the United States. However, lynx were often distinguished from bobcats in historical or bounty record some confusion exists in regard to the southern extent of the fo range. Historical records indicate that lynx were found in lov moderate densities throughout forested sections of Wisconsin, York, Vermont, New Hampshire, Maine, Nova Scotia, and Newfo land (Orff 1985). Similar densities were present in the western m tains as far south as Oregon and Colorado. Local lynx populatior other parts of Canada and Alaska probably have experienced dec due to agricultural, industrial, and suburban development, but t declines could be considered relatively minor compared to t caused by habitat loss in the northern United States and southea: Canada.

However, from 1880 to 1920, a time included in the heigl wild-fur trade, successive peaks in the lynx cycle showed conti declines (Todd unpubl. report). Throughout this period each new in the lynx harvest was lower than those preceding it. In the late 1 about 80,000 lynx were pelted, but by the early 1900s the nu had dropped to 20,000 (Todd unpubl. report). This trend conti through 1940.

The available evidence suggests that a major decline in lynx abundance occurred during a period of less than 30 years around the turn of the century, when fur-trade trapping was basically unregulated on the western frontier. Intense exploitation is seen as the primary reason for the lynx decline (Elton and Nicholson 1942, Devos and Matel 1952). Pelt prices remained stable throughout this period, so a lack of economic incentive was not responsible for the smaller fur harvests.

Lynx were considered pests in the early 1900s and attempts were made to control their numbers. Bounties were still offered in some states in the 1960s, but lynx are no longer considered undesirable (Siegler 1971).

CURRENT TRENDS

The lynx had re-occupied much of its former range by the early 1960s. These gains continued into the early 1970s, but data now indicate that the occupied range has shrunk again (Todd unpubl. report).

In the early 1980s, lynx were present in 14 states and all Canadian provinces and territories except Prince Edward Island (Deems and Pursley 1983). Accurate, or even rough estimates, of lynx numbers do not exist because of this cat's secretive nature, generally low densities, and confounding population dynamics. However, the best compendium on the status of the lynx in North America can be found in Jorgensen and Mech (1971). Status reports are included for Alaska, British Columbia, Saskatchewan, Wisconsin, New Hampshire, and the northwestern states. These reports suggest that trapping was not the only factor involved in local declines of lynx populations. They also indicate that, in general, lynx populations are secure in Canada and Alaska, but withdrawing from the heavily human-populated southern fringe of the species' range. State reports from New England, New York, Wisconsin, and Wyoming indicate that lynx are present but in very low densities.

Research in Canada and Alaska indicates that increased trapping pressure and habitat alteration and destruction are still having negative impacts on lynx populations in some areas. This is particularly true for lynx along the southern edge of the range, where densities are low and access to trap lines is high. The implications seem to be that heavy trapping, spurred by large jumps in pelt prices, is largely responsible for the decline in lynx abundance throughout much of the range. Only remote regions in the Yukon and Northwest Territories have shown actual increases in the latest cyclic peaks compared to previous peaks

(Todd unpubl. report). Habitat loss is considered of secondary importance and is probably more critical along the southern edge of the range.

Some researchers believe that intense trapping when lynx are at low levels could be a form of additive mortality, removing adult lynx that normally would survive during the cyclic lows and reproduce when snowshoe hares increase (Brand and Keith 1979). A similar increase in mortality also could occur when adult lynx are isolated in "pockets" of suitable habitat and adequate food supply during low density years, especially if large numbers of trappers have access to these pockets (Berrie 1974, Todd unpubl. report). Maintaining an adequate breeding stock during low population years is critical to ensure a swift and substantial increase in lynx numbers during the increase phase of the 10-year cycle. If this management objective is not attained, the major long-term impact seems to point toward lynx populations that cycle about a lower mean level and that show markedly reduced population peaks.

Although trapping and poisoning of lynx were once widely practiced in Europe and Russia, regulated hunting and trapping seasons now exist. Scandinavian and Finnish-Russian lynx populations are once again becoming contiguous, possibly because of reduced hunting, better food conditions, and reduced competition from wolves. Reintroduction of lynx has been carried out in parts of Germany, Austria, Switzerland, Italy, and Yugoslavia (Heggberget and Myrberget 1980, Smit and Van Wijngaarden 1976).

The Spanish lynx is classified as endangered and is confined to isolated, mainly mountainous areas in central and southern Spain and Portugal. The total population is estimated at 1,000 to 1,500, but is rapidly declining because of habitat loss, disease, and accidental kill (Delibes 1979).

MANAGEMENT

Lynx management generally focuses on regulating the yearly kill, with trapping and hunting confined to specified seasons during the winter months. In Canada, trappers are required to operate on registered trap lines or areas. In Washington, lynx can be pursued with hounds on a limited basis and both trappers and hunters are required to register lynx pelts with the Department of Game. Currently lynx are subject to limited harvest in six states and 10 provinces and territories and are receiving total protection in nine states and one province. The lynx is on the endangered species lists of Colorado, New Hampshire, and Wisconsin and is listed in Appendix II of the Convention on Inter-

tional Trade and Endangered Species of Wild Flora and Fauna treaty (Defenders of Wildlife 1984), giving it some protection from the international fur trade.

Many states and provinces currently are monitoring or planning to monitor lynx populations. Private organizations, such as Defenders of Wildlife, urge that the status of the lynx throughout its range be carefully monitored and that management be reevaluated, taking into account the rise in pelt prices (Defenders of Wildlife 1984).

Published accounts on habitat management for lynx are scarce. Research is being conducted in the northwestern states to determine habitat use and to evaluate the impact of timber harvest on lynx distribution on national forest lands.

PROGNOSIS

Research suggests that lynx populations are relatively stable throughout much of the North American range. However, in some regions local populations have declined to levels lower than the apparent normal cyclic lows of the recent past. Many researchers believe that more effective management will have to be developed and applied if exploitation of this species increases. The extreme fluctuations in numbers, coupled with the ease with which the species can be trapped, could contribute to severe local reductions of breeding stock. Although the lynx may be considered safe throughout much of its range, populations levels should be watched closely. Increasing economic value of lynx pelts could influence pressure on local populations (Jorgensen and Mech 1971).

The influence of pelt value on lynx harvests is of critical importance. As recently as the 1984-85 season the price on a prime lynx pelt soared to over $1,000. Average pelt price was $650 (Haefer, Moscow Hide and Fur, pers. comm.). With price tags such as these the incentive is created to sacrifice conservation and long-term economic productivity for short-term economic gain (Todd unpubl. report).

It is possible that local populations, and possibly populations over broad parts of the range, will decline if pelt prices continue to rise and trapping pressure intensifies along with increased habitat loss. Some biologists believe that these trends will continue and, therefore, that the concept of a lynx surplus suitable for trapping will have to be reevaluated (Bailey unpubl. summ.). They also suggest that new management strategies for lynx need to be developed because lynx occur in fluctuating and highly unpredictable environments, cycle over eight to 11 year periods, usually are dependent on hares as their sole source of food, and are highly vulnerable to trapping, especially in accessible areas.

One management strategy that has been suggested is to curtail or cease the taking of lynx for three years during the declining phase of the 10-year cycle (Brand and Keith 1979). During this time, recruitment of kittens into the population is very low or nonexistent. The surviving adults therefore play the extremely important role of restocking the population. Reducing trapping mortality for three or more years during the population phase decline would lessen the population crash. In highly accessible areas with few natural refugia, curtailment of trapping up to five years, followed by quotas or shortened seasons, may be necessary to prevent overexploitation (Bailey *et al.* 1986).

Other factors have been named as possible agents involved in reducing lynx abundance. Habitat loss, severe winters, industrial development, and snowshoe hare population levels have had some localized influence, but only contributed a fraction of the total impact.

It is unlikely that the lynx will be classified as endangered throughout its range in the foreseeable future, but it may become increasingly rare in areas accessible to large numbers of trappers and susceptible to habitat alteration or destruction. What is likely is that increasingly stringent trapping regulations will be needed in some areas to ensure that viable local populations continue to exist at or near carrying capacity. A drastic drop in fur prices could improve the outlook in heavily trapped areas.

RECOMMENDATIONS

Theodore N. Bailey recommended that ideal lynx management should be (1) highly flexible, (2) rapidly responsive to sudden changes in lynx habitat or prey abundance, (3) able to predict the impact of trapping on the entire lynx cycle rather than only on the following year's population, (4) closely tied to snowshoe hare abundance and distribution, (5) able to consider offspring dependence on females by adjusting trapping periods, and (6) able to provide for adequate stocks and distributions of breeding adults during years of low prey abundance (Bailey unpubl. summ.).

Several trapping regulations have been suggested. These include closing the season for three to five years once lynx and hare populations have peaked, shorter and later seasons, quotas and permits based on management areas, untrapped sanctuaries, and perhaps restricting the use of exposed bait, flag, and cubby sets during other furbearer seasons to reduce incidental lynx capture (Bailey *et al.* 1986, Brand and Keith 1979). Continued and improved monitoring of lynx populations throughout the range is essential to developing proper base-line data from which management decisions can be made.

In 1978, several biologists reviewed whether international trade in species listed under Appendix II of CITES was detrimental to the survival of those species (Mech 1978). They recommended that each state review its lynx research and management programs and seek to improve them in order to help ensure continued lynx survival. This directive still can be considered a timely one today.

Virtually every aspect of lynx biology, ecology, and management is in need of further research. The impact of trapping, habitat alteration, and human interference on local population levels and social organization is vital to the management of this species, especially on the southern edge of lynx range where numbers may be declining. Studies designed to remove certain individuals and to manipulate habitat could provide answers about man's influence on lynx populations. Individuals which are taken from a population during removal studies could be introduced into low-density areas, thereby providing information on possible stocking programs. Concurrent studies on lynx and bobcats could help determine whether the species compete for the same resources or if they are ecologically separated by differences in adaptation or habitat preference. Additional basic knowledge of social organization, predator-prey relationships, and habitat preference also is needed.

The challenge of lynx conservation and management is a multifaceted one. Pelt values and the fur harvest, the 10-year cycle, survival, mortality, changing reproductive parameters, and habitat loss all play a part in the population dynamics of this native cat.

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U.S.S.R. (Sunquist 1981). In spite of this wide variation, however, where prey abundance is comparable and stable over time smaller cats have smaller home ranges than larger ones. The enormous variation in home range size when one views an array of feline species is in fact related to the temporal and spatial distribution of the prey items and the mean body size of the species. In areas with stable populations of wild felines, the density may vary widely as varies the carrying capacity. In general, cats distributed at higher latitudes tend to have larger home ranges than their near relatives or conspecifics living in warmer latitudes (Kleiman and Eisenberg 1973).

A home range is not uniformly used and indeed different activities may be carried out in different portions of the range. This is especially true if shelter happens to be limiting. Resting may be in a different location on consecutive days (Sunquist 1981), or local site preferences for resting may be shown in certain environments. Smaller cats, such as the bobcat, may shelter in small rocky areas and use these areas almost exclusively during heavy rain (Zezulak and Schwab 1980). The larger cats in tropical climates are less prone to seek shelter such as rock caves, hollow trees, or abandoned burrows as smaller cats do. Indeed, the larger, tropical cat's primary requirement is not so much shelter from rain but rather shade to avoid direct sunlight and overheating.

The question of territoriality or exclusive use of a land area by an adult has been a vexing one and variation is shown when the family Felidae is surveyed. As a rule, juveniles until the age of adulthood are tolerated within an adult's home range. Upon attaining puberty, however, the young animals disperse and become transient until a suitable, unoccupied portion of the habitat can be found where they may begin to establish a home range and eventually defend it.

Adult females are potential competitors with one another for appropriate space in which to hunt prey and rear their young. Adult males are potential competitors among themselves in that they compete with one another during the breeding season for access to estrous females. Thus, males will tend to defend an estrous female from other males. The outcome of these first order interactions is a simple one; namely, that adult females tend to be rather uniformly spaced in the environment and male home ranges overlap a female's so that the male maximizes his access to estrous females and attempts to exclude other males from the area. The degree to which this ideal scheme can be achieved in practice depends on the cost in energy expenditure to the male or the female in attempting to exclude possible competitors of the same sex. Because home range size varies depending on the prey density, the season of the year, and the climate, resident animals may be incapable of defending a home range area sufficiently well to exclude possible competitors. This accounts for most of the cases where overlap exists in the home ranges of like sexed adults. Overlap occurs when the cost of excluding the neighbor is either too great or, if the home range is large enough, impossible.

Some cases of home range overlap among females may occur as a result of settlement of a female offspring on either a portion of the mother's range

or close to her. Thus, some contact between two relted females may be maintained and spatial use patterns can be coordinated. Such a case has been described for the tiger by Sunquist (1981).

Advertisement of presence on a home range or territory is usually accomplished by urine spraying, tree scratching, or the emission of a long-range call. Urine spraying can serve not only to demarcate a home range use pattern, but it may also indicate sexual condition to individuals of the opposite sex. Long-range calling can serve a similar advertisement function. Communication in the Felidae has been extensively reviewed elsewhere (Wemmer and Scow 1977; Leyhausen 1979; Peters 1978).

Lions are among the most sociable of the felines and exhibit an interesting variation on the basic feline pattern. In habitats with a reasonably high carrying capacity, females may remain together in a pride and communally hunt as well as communally defend their litters. Some of the females may even be related by descent; thus, a kin system among the females can be set up. Male lions either singly or in cooperation with a partner will attempt to oust resident males and take over the pride of females, thereby ensuring access to estrous females on a continuous basis (Bygott et al. 1979; Bertram 1978).

Another interesting variant on the land tenure system in the short to medium grasslands of the Serengeti is displayed by cheetahs (Frame 1980). Females have enormous home ranges, due in part to the fact that the prey species are seasonally abundant and to some extent migratory. Since the female has the responsibility of rearing cubs and hunting for them, she must have a large range to have continuous access to prey. Because the range is large, she makes no attempt to defend it. On the other hand, males not having the same energetic demands placed on them may choose a habitat with a more permanet prey base and in more wooded areas and thereby defend a territory to the exclusion of other adult males. Home range sizes for single males may vary between 12 and 36 km². Because the males select the more wooded fringe areas adjacent to the short grass prairie, the territories of males may be somewhat clumped in space (Frame 1980). Thus, when viewed in a "macro" sense the territories of the males approximate a quasi-lek as outlined by Bradbury (1981). The picture that the cheetah presents in this particular part of Tanzania is exactly what Bradbury would have predicted from this discussion of the evolution of lek breeding systems. Namely, that when the nutritional requirements of females in a given habitat predispose them to have enormous home ranges that are undefended, then it is impossible for a male to monopolize a group of females by defending their ranges and instead the males will begin to optimize the microhabitat for themselves and create a mutually exclusive land tenure system to which females will come to be bred. The cost to males of clustering in a particular habitat type must be equalled by the preference of females for clusters of males because the females then have the ability to choose among territory holders with respect to breeding. That this is only one form that the distribution of cheetahs may take in space is clearly demonstrable from other studies on the cheetah (McLaughlin

1970; Schaller 1972; Eaton 1974), where there is no indication of territorial defense and more than one male can actively attempt to join an estrous female prior to mating.

Where the land tenure system involves fixed territories interference by other males during mating is eliminated. However, where the land tenure system shows overlap in home range several males may be attendant to an estrous female. Fighting among males to establish dominance and priority of access to females is not unknown in the bobcat and the lynx. On the other hand, males that apparently "know" one another or have a preestablished dominance order can avoid fighting when in the proximity of an estrous female. In a highly social felid such as the lion, however, a lioness in estrus may mate with more than one male associated with the pride (Schaller 1972).

As a rule the major burden of rearing the young and provisioning them with food until they can learn to hunt falls to the female. Males may indirectly ensure that the maximum resources are available to the female if they exhibit territorial behavior and can exclude other males from the female's home range, thereby reducing direct competition for prey. The only known instances of males providing food for females and cubs are those data derived from observations on lions (Schaller 1972; Bertram 1978). Captive observations have indicated male tolerance for cubs and in some cases food sharing by males with their young has been noted (e.g., the black-footed cat, *Felis nigripes;* Schürer 1978).

Epilogue: Canids and Felids Revisited

I would now like to compare and contrast the reproductive adaptations of the family Canidae and the family Felidae. With the exception of the Mustelidae or weasel family, these two families represent the most highly evolved predatory groups and the larger species of both families can take down prey animals many times their own body weight. Some species of the family Felidae are larger than those of the family Canidae, but within both families there may be extremely small species less than 5 kg in weight. Typically, larger species of mammals have smaller litter sizes and longer intervals between litters. Therefore, all discussion of litter size and reproductive potential have to be cast against the background of the different size classes that we can discriminate within the two families. Within any given size class, canids generally exceed felids in terms of the number of young produced (see Table 1). The female lions produce litter sizes slightly larger than would have been predicted from a knowledge of their body size. This relates to the unique social rearing pattern of the lion which differs markedly from most other cats as discussed previously. With the exception of the lion then, if the breeding of a felid or canid species is tied to a restricted portion of the year, in general the canid species has the ability to rear more young in a shorter period of time. Canids can then take advantage of short term fluctuations in the food supply. If, however, we attempt to forecast the annual productivity of canids

and felids within the same size class, then there are two features that must be considered. First, within both families as we proceed from the pole towards the equator the breeding season is less restricted. In the tropics the breeding season is usually longer. This occurs because primary productivity is usually very closely constrained in time toward the poles, and it is during this period that the female attempts to rear her young and maximize their initial growth. In the tropics there is a relaxation in the discrete timing of primary productivity although it may be pulsed. As a result there is a relaxed selection pressure for a restricted breeding season. It does not follow, however, that the timing of breeding in the geographically defined tropics is totally relaxed. Over vast areas of the tropics breeding is highly controlled by primary productivity which in turn is controlled by rainfall. Rainfall within 21° to 10° north and south latitude can be highly variable depending on the size of the land mass, proximity to the coast, or presence of mountains. The net result is that not only do we have annual variation in rainfall that controls secondary productivity, but we have coupled with this vast differences from one year to the next in not only the total amount but the monthly rate of rainfall. Areas subjected to periods of 4 to 5 months with no rainfall exhibit pronounced seasonal variations in productivity that can modulate the onset of reproduction from one year to the next. These fluctuations can also exert considerable regulation on the survivorship of young born in any given year. The only amelioration within these latitudes for the seasonal rainfall effect involves riverine or lacustrine habitats. Here, conditions often are more predictable than in upland areas and areas away from permanent rivers.

In the north temperate zone, ovarian activity in both canids and felids may be sharply seasonal. As one proceeds toward the tropics, however, the periodicity of ovarian function may be relaxed so that tropical felids may potentially breed in any month of the year. For many canids that have invaded tropical habitats, however, ovarian function is still to some extent seasonal; the only known exceptions to this rule are the ovarian cycle of the Cape hunting dog *Lycaon* and the South American bush dog *Speothos* (Porton et al., in press). Both *Lycaon* and *Speothos* can show a higher annual productivity of young than comparable size canids in the temperate zone. All things being equal, no annual productivity of any tropical felid approaches that of *Speothos* and *Lycaon*. *Speothos* has a reduced average litter size (3.5) but the female can come into heat upon weaning her young and produce 2 litters in one year. It therefore seems safe to say that over a wide latitudinal range including both the temperature zone and the tropics, canids have the capacity to produce a higher number of young in a given year than a felid within the same size class (see Table 1).

The behavior patterns of the larger canids and felids also stand in marked contrast. As indicated in the previous section, the hunting strategy is quite different. The cursorial habits of canids allowed them, as they evolved a larger body size, to evolve group methods of hunting in running down prey larger

than themselves. On the other hand, the large felids have clung to the hunting system based primarily on individual hunting tactics, concealment, sudden rush and dispatch of the prey. All of this reflects a fundamental difference when the social systems of canids and felids are compared and contrasted.

Almost all canid species base their rearing system on a bond between an adult female and an adult male. Kleiman and Malcolm (1981) have reviewed the distribution of parental care within the class mammalia. Their conclusion is that although certain forms of parental care have been reported for some species of felids, the canids dramatically exhibit a uniformity of parental care during the rearing phase by the female. During the lactation phase, most female canids receive some form of direct or indirect provisioning from the male. That a female can raise a litter in the absence of a male is not to be disputed, but surely her rearing success is a function of the number of helpers that she has (Malcolm and Marten 1982; Moehlman 1983). Not only may the male provision the female, but a litter of a previous year may also participate, and the rearing success of the female definitely seems to be tied to this (Moehlman 1983).

The most complicated form of cooperative rearing strategy found within the Canidae occurs within the Cape hunting dog, where sibling groups of males may emigrate to set up a new territory with an unrelated female and as a group participate in rearing her offspring even though only one of the brothers mates with the female. Nothing quite comparable to this degree of paternal investment is found within the Felidae. The lion does live in groups and cooperative hunting is shown. In the lion, the stable element of the group is a set of females that may be related by descent. Such a group comes under "protection" of a group of adult males and their rearing success is exhanced until such time as a takeover by an alien group of males results in loss of all their young cubs (Bygott et al. 1979). Variations on rearing success and sociability have been discussed by Bertram (1978).

When one compares the two families then, in canids, litter size can be increased for a given size class of females in part because of the paternal care behaviors shown by the male. This allows great flexibility within most species of canids to take advantage of short term fluctuations in productivity and respond by the rapid production of young. In contrast, the more solitary way of life exhibited by most feline species results in a lower annual productivity by the female and a reduced ability to rapidly adjust to changes in carrying capacity. As a generalization one could say that felids are more K selected relative to the canids or conversely that the canids, for the most part, exhibit a higher degree of r selection. The implications for management of this suggestion are quite clear. Populations of canids can recover rapidly from short term fluctuations in prey base, epizootics, or exploitation pressure. On the other hand, the felids show a somewhat reduced capacity to respond quickly when their populations decline. These generalizations should be borne in mind when conservation plans are developed for the two taxa.

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Forest Fires and the Snowshoe Hare-Canada Lynx Cycle

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Summary. This paper shows that there is a reasonable coincidence between the Canada lynx cycle and the occurrence of forest and brush fires. Fires set in motion plant succession, potentially leading to an increase in snowshoe hares (Grange, 1965). Snowfall is also correlated with the lynx cycle and tends to account for the variation not accounted for by fires. I conclude that Grange's (1949, 1965) hypothesis that fire and plant succession drive the snowshoe hare cycle deserves serious consideration, as do Butler's (1962) and Watt's (1968, 1973) suggestions that precipitation may drive or decisively modify furbearer 'cycles'. On this evidence, the snowshoe hare-Canada lynx cycle seems likely to be a forced oscillation rather than a predator-prey, parasite-host, or herbivore-vegetation limit cycle, as proposed by several authors. Fire clearly appear to be a periodic phenomenon, notwithstanding the difficulty of showing periodicity in simple weather time series. Fire is itself a meteorological phenomenon, although complexly related to simple weather variables.

Introduction

Canada lynx fur returns, and pelt returns of many other fur-bearing mammals in Canada, have exhibited remarkably periodic fluctuations for over 100 years (Keith, 1963; Butler, 1953; Elton and Nicholson, 1942a; Seton, 1912). The lynx is almost wholly dependent upon snowshoe hares as prey (Seton, 1953; Keith, 1963; Nellis et al., 1972), and the approximately 10-year periodicity of the lynx and some other predators seems almost certain to be driven by corresponding population changes of the hare (Keith, 1963; Bulmer, 1974; Brand et al., 1976). The hare is the only herbivorous mammal exhibiting a 10-year periodicity, with the possible exception of the muskrat (Elton and Nicholson, 1942b), which seems capable of driving oscillations of furbearing predators. Reliable data on the snowshoe hare (MacLulich, 1937, 1957; Keith, 1963)

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span a shorter time period in a much smaller area than the lynx data. Hence lynx pelt returns are used here, as in previous studies, as a measure of both lynx and hare fluctuations. The impossibility of using contemporary rabbit fur returns has been discussed by Keith (1963, pp. 9-19, 66, 119).

Possible causes of the Canadian furbearer cycles have been discussed most extensively by Keith (1963). Moran (1953) suggested that the hare-lynx cycle is a predator-prey oscillation, but Keith (1963, p. 115) gave convincing evidence against this, and Butler's (1942) work strongly reinforces his conclusion. For Lack's (1954) suggestion of a rabbit-vegetation oscillation, or Gilpin's (1973) idea of a host-parasite oscillation, there is no decisive evidence. Because of the regularity of the lynx fur cycle, the idea that it is some kind of limit cycle caused by the interaction of two or more species has dominated ecological discussions. So far no external forcing function has been found (Keith, 1963: pp. 102-7) which might drive the cycle. However, Watt (1968, p. 155) pointed out a possible relation between hares and snowfall over three 'cycles,' and showed a negative correlation between juvenile hare survival and snowfall (Watt, 1973, p. 128). Butler (1962) found significant correlations between muskrat pelt returns and precipitation in Saskatchewan.

Grange (1949, 1965) proposed that snowshoe hare fluctuations are caused principally, though not exclusively, by fluctuations in the extent of post-fire successional habitats containing the hare's essential or optimal foods. This hypothesis can overcome some of the difficulties encountered by Bulmer (1974, 1975) in explaining correlated 'cycles' among a variety of species.

For one or more years after a fire, food and cover are reduced and hares might abandon the site (Keith and Surrendi, 1971; Grange, 1949). As post-fire succession proceeds in the boreal forest regions, either jack pine or deciduous shrubs and trees like birch, aspen, and willows increase in biomass and productivity (Grange, 1949, 1965; Rowe, 1959, 1966; Heinselman, 1973; Ahlgren, 1974; Hardy and Franks, 1963). The seedlings are at first below the winter snow line and are not available to hares as winter browse; much later their buds and small twigs will grow beyond reach; in the meantime there occurs an interval of maximum availability and productivity of buds and small twigs which are above the snow line and within reach of hares (Grange, 1965; Bider, 1961; Pruitt, 1970). The hare's principal food plants are post-fire successional species of the boreal forest regions, as documented later. Grange (1949), Edwards (1954), and Heinselman (1973) noted the relations of other animal species to post-fire plant succession.

Fire governs boreal forest vegetation diversity by reinitiating plant succession at frequent intervals, creating a successional mosaic (Heinselman, 1973; Viereck, 1973; Rowe and Scotter, 1973; Rowe, 1966; Hardy and Franks, 1963). Recognition that lightning fires are a natural, ancient, and constantly recurring influence in boreal forest regions is a relatively new and important contribution to vegetation ecology. No region of the North American boreal forest is free from recurring forest fires which are either more frequent or larger than those farther south (U.S. Dept. Agric., 1921-1974; Forest Fire Losses in Canada, 1948-1969; Hardy and Franks, 1963). However, it has never been established whether fire occurrence is quasi-periodic, with the exception of an apparently forgotten paper by Mitchell and Olsen (1954).

Methods

Data sources were as follows: Lynx fur returns are taken from Elton and Nicholson (1942a) for 1821-1933, from Keith (1963, Table N) for 1919-1957, and from Canadian government fur reports (Statistics Canada 1958-1973) for later years. The area burned in Canada is from Forest Fire Losses in Canada (1948-1969), and from data compiled and sent to me by the Forest Fire Research Institute, Department of Environment, Ottawa, Canada, for 1929-1947 and 1970-1974. The fire data which I have used is total area burned, including both the 'forested' and the 'nonforested' categories of Forest Fire Losses. The two categories are well-correlated in trend. Lynx fur returns for 1821-1934 for the Mackenzie River District of the Hudson Bay Company were keypunched directly from Moran (1953), but were originally compiled in Elton and Nicholson (1942a).

Figure 1, covering historical records of fires, 1820-1973, comes from the following sources: On the left of scale A are subjective ratings by Elton (1942) of 'big' (XXX), 'big?' (XX), and other (X) fires noted in early manuscripts and journals from northern Quebec and Labrador. On the right of scale A is area burned annually (full scale $\frac{1}{2}$ million acres) within 53 million acres of U.S. Forest Service lands in Montana, Idaho, and northwestern Wyoming, for 1908-1939 (Barrows, 1951).

On the left of scale B is data from Plummer (1912). The full scale represents 2 million acres burned. Plummer searched official documents for all U.S. states and territories and for the southern Canadian provinces. His Canadian fires are entirely different from those reported by Elton (1942). Fires before 1870 are based upon only one reported large fire each year, while in 1871, four reports contribute, with increasingly more reports from many states and provinces in later years. I recorded only fires which Plummer reports from southern Canada and from the northern tier of U.S. states having borders with Canada. The 'X' on this scale records Heinselman's (1973) note of fires raging near Winnipeg in 1863-64. In scale B on the right are numbers, not area, of fires in the Lake States (Minnesota, Wisconsin, and Michigan) as reported by Mitchell and Olsen (1954). They presented the data as percentage deviations from the mean, computing a different mean for five successive eight-year periods. Numbers of fires are correlated ($r > 0.50$) with area burned in these states. The full scale spans 50% to 150% of the mean. The 'X' records the 1918 Cloquet, Minnesota, fire, which was enormous and occurred in an exceptionally bad fire year in general (Haines and Sando, 1969). It is unclear whether this fire was included in Mitchell and Olsen's (1954) report, as much of the fire was not on Federal lands.

Scale C gives Heinselman's (1973) estimate of area burned in the more than 1 million acre (ca. 1560 square mile) Boundary Waters Canoe Area at the Minnesota-Canada border, as estimated from the areal dispersion of dated tree fire scars. The full scale is 100 square miles. Scale D gives the number of independent studies demonstrating a pronounced minimum in tree-ring growth, from seven different studies on eastern hemlock in New England (Lyon, 1946). The full scale is five coincident reports of a pronounced minimum. Minima were selected subjectively by Lyon, but examination of the data in Lyon's sources should convince the reader that the minima which Lyon called 'pronounced' (the only ones which I used) would be selected by most observers. Ring-width is correlated with the preceding year's precipitation as much or more so as with current precipitation (Fritts, 1962; Zahner and Stage, 1966), so Lyon's data is plotted 1 year before the tree-ring dates. Tree-ring data are quite relevant because remarkable fire years coincide with 3-8 month droughts (Haines and Sando, 1969; Heinselman, 1973), and tree-ring width reflects evapotranspiration (Fritts, 1962) and plant water potential (Zahner and Stage, 1966).

The scale second from top in Figure 1 contains, on the right, the same Canada fire data as in Figure 2. The full scale represents 4 million acres. On its left, the X's note coincidences of three or more prominent fire years on the four scales below. This is an attempt to decide whether 'big' fire years occur synchronously over large areas, and whether or not they coincide with the lynx fur cycle (top scale). Because of the varying reliability and heterogeneity of the historical data, primary weight should be given to broad geographical coincidence, i.e., occurrence on several scales, rather than to absolute size of fires on one scale. Plummer's (1912) data after 1870 (Scale B) are sufficiently general for this purpose even without the other data.

Autocorrelations and smoothed spectral estimates were computed following Jenkins and Watts (1968). Series were converted to logarithms to better approximate normality. Residuals about the linear regression line for the logarithms were used as the time series for computing spectra and autocorrelations. Smoothed spectra were compared at lag-window lengths of 4, 8, 16, and 32

(bandwidths of 0.3333, 0.1667, 0.0833, and 0.0417 in cycles per year), using a Tukey window. Instability owing to high variance of the estimate was evident only at the smallest bandwidth. Resolution of the 8–12 year component naturally increases as bandwidth narrows. Autocorrelations and spectra were computed for the annual data and for moving averages of 2, 3, 4, 5, and 6 years in length. A moving average of 3 years was sufficient to filter out most of the 2–3 year quasi-biennial fluctuation. A moving average of length M introduces an autocorrelation of $r_L = (M-L)/M$ at lag L, into an otherwise random series (Kendall, 1973), which falls to zero at lags beyond (M-1). The mean interval between peaks introduced by such a moving average should be about 4 years; this 'Slutzky effect' is evident just barely if at all in the spectra. Autocorrelations show that the residual time series may be non-stationary, although sample sizes do not really permit a firm conclusion. Non-stationarity may affect the robustness of statistical tests. However, the residuals did not differ from normality using skewness and kurtosis as criteria, and this is more important for significance tests (Jenkins and Watts, 1968).

Cross-correlations and cross-spectra between lynx and fire time series were not computed. The biologically reasonable time lag between hares and fire is at least 5 and more likely 10–20 years, reducing sample sizes unacceptably.

Extensive correlation and regression analysis of lynx-fire-precipitation relationships have been started. Only preliminary results are presented here. The SPSS statistical package has been used extensively, and has proved quite useful. Fire variables tested are 1–5 year moving averages of area burned annually, lagged from 0–23 years in the past. Precipitation variables tested are the sum of precipitation for December through February, November-March, May–June, and May–July, for 0–3 years previous to the winter of lynx trapping; and the 2- and 3-year sums precipitation during each of these four calendar periods, i.e., sums for the calendar year of the winter of trapping plus one or two previous years, for the precipitation period in question. These sums were lagged 2 and 3 years, extending the actual lag back 4 and 5 years in effect.

Snowshoe hare hunting-kill estimates for the Lake States were obtained from Keith (1963, pp. 150, 160) through 1957 and directly from state game departments for 1957–1974. These were divided by the number of small game licenses sold the same year, to give a snowshoe hare index after the fashion of Keith (1963, p. 39). Both the kill estimates and the index are approximately normally distributed. I carefully compared the gross bag estimates with the index; the variance appears lower for the index than for the kill estimate. Their trends appear very similar except for recent years in Michigan, for which the rise in snowshoe hares killed was extremely rapid, increasing faster than the index. Since 1968, the number of hunter-days spent in pursuit of snowshoe hares in Michigan has been estimated, and dividing the kill estimate by this number gives an index almost exactly 10 times the index found by using hunting licenses as the divisor. I have thus used 1/10th this hunter-effort index for the period 1968–1974. The divergence of the two indices in Figure 6 indicates the possible errors in such indices, underscoring Keith's (1963, p. 12) warning about interpretation of them. Forest fire data come from Forest Fire Statistics (U.S. Dept. Agric., 1921–1974).

Results

Figure 1 demonstrates a fair correspondence between fire history and the lynx cycle over the past 150 years. The record of fires is very patchy and inadequate before 1860, 117 years ago. There were outstanding fire years in 1853–54, 1863–64, 1870–71, 1880–81, 1893–95, 1902–03, 1910–11, and 1917–19. This 10-year pattern continues from the time accurate estimates are available for Canada, with peak fire years in 1925–31, 1937–42, 1948–50, 1961, and (?) 1970–71. These fire years precede peaks or coincide with troughs in the lynx cycle. In two cases, 1874–75 and 1933–34, fire years coincide with lynx peaks instead of troughs, and in these cases, the fire years appear to be regionally confined.

I obtained Kendall rank correlation coefficients (τ) between the fire histories in Figure 1 and the lynx cycle by using lynx data for the Mackenzie River
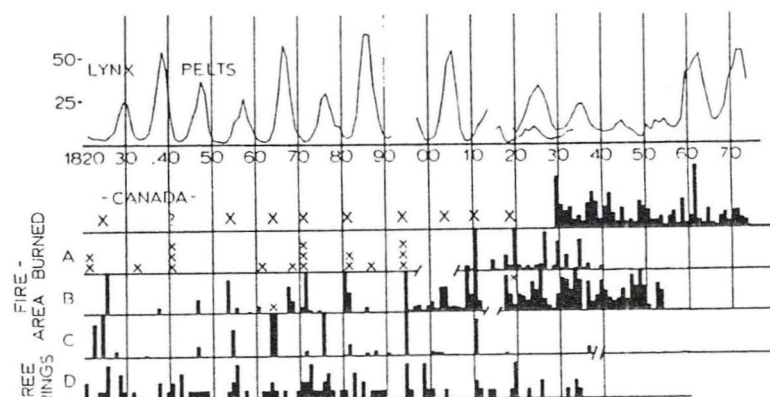
Fig. 1. The historical record of forest fires and some tree-ring minima in the United States and Canada, compared to the lynx cycle. Data are explained in 'Methods' and statistical tests given in 'Results'. On the scale marked 'Canada', X's mark coincidences of peak fire years in different regions on the scales below, until 1929, when data become available in Canada

District, which presents the longest unbroken series and which follows the lynx series for all of Canada very closely (Elton and Nicholson, 1942a). For Plummer's (1912) forest fire data, on scale B in Figure 1, $\tau = +0.176$ ($P = 0.015$, $N = 91, 1821-1911$), between lynx and area burned 2 years previous. For a composite fire and tree-ring index, obtained by normalizing data on scales A–D to the range 1–10 and summing them, $\tau = +0.16$ ($P = 0.028$, $N = 74$, 1821–1894), between lynx and the index 2 years previous. In both cases lags of 0–9 years were tried. The maximum correlation with snowfall (precipitation for November through March), in Edmonton, Alberta was found for the sum of precipitation during two previous years, $\tau = +0.166$ ($P = 0.045$, $N = 50$, 1885–1934).

Area burned over a large area in Canada exhibits considerable similarity to the trend of the lynx cycle (Fig. 2). Aside from the apparent periodicity in area burned, especially for a moving average or sum, there is a common downward trend. However, this common trend is probably spurious, and it is argued below that lynx declined owing to overexploitation. The scatter plot at upper left in Figure 2 shows the relation between lynx pelt returns and the 4-year sum of area burned 15–18 years previous. As discussed below, only the last 19 years of lynx data (1955–1973) appear to be appropriate to this analysis. For those years, the maximum correlation is $r = -0.83$, with the 4-year sum of area burned at 16–19 years in the past ($P < 0.001$).

The smoothed spectra (Fig. 3) exhibit a very remarkable correspondence between the periodicities of the lynx and fire time series. The fire data are all the more remarkable because, to the best of my knowledge, no other meteorological time series has yielded such a pronounced peak (Lamb, 1972; Currie, 1974; Mock and Hibler, 1976). All spectra in Figure 3 differ significantly ($P < 0.001$) from expectations for a random normal (white noise) process in the interval 9–11 years. The lynx data, but only these data, had to be detrended
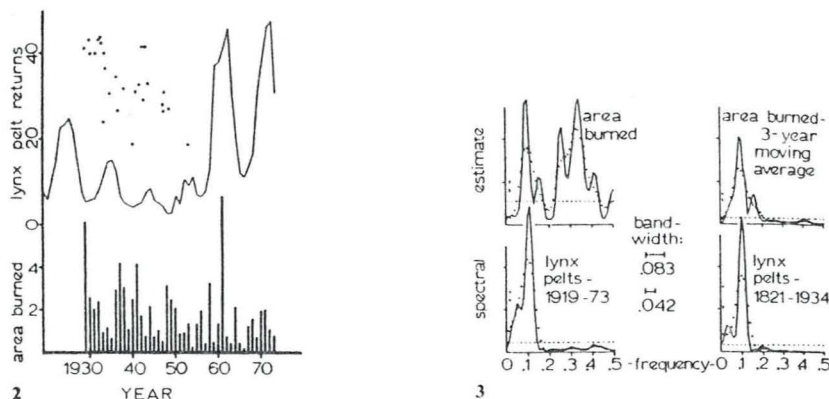
2

YEAR

3

Fig. 2. Annual Canada lynx pelt returns (*upper, solid line*) for 1919 1973, area burned annually 1929 1973 (*below, histogram*), and a scatter plot (*upper left*) of the logarithm of annual lynx pelt harvests against the 4-year moving average of area burned 15 18 years previous ($N = 26$, $r = -0.63$, $P < 0.001$). The data are for British Columbia, Alberta, Saskatchewan, Manitoba, Ontario, and Quebec, combined. The three outliers on the lower left of the scatter plot, for lynx in 1949 1951, followed 4 years, 1947 1951, of the highest snowfall for this period; the two outliers at upper right, for lynx in 1959 60, follow three years in a row of very low snowfall in 1958 1960, in Edmonton, Alberta. There are some other years of comparably low snowfall, but these are isolated rather than sequential. In Moosonee, Ontario, there is less direct correspondence between these outliers and snowfall, but low snowfall occurred in 1959 1960, and high snowfall occurred in 1943 46, 1948, and 1950 51, in succession. 'Snowfall' above refers to the sum of snowfall in one year plus the two preceding winters, i.e., a 3-year moving average or sum.

Fig. 3. Estimates of the variance spectra for area burned in Canada and lynx pelt returns for Mackenzie River District (1821 1934) or for the lynx data of Figure 2 (1929 1973). *Carats on the left* show lower 95% confidence limits for the peaks at 10 11 years, the lower of a pair being for the lower (0.083 bandwidth) peak. The *two upper figures* compare area burned (*upper left*) to its 3-year moving average (*upper right*) to show how this simple filter removes the 2 3 year 'noise', derived from the quasi-biennial fluctuations in precipitation, most likely. Such a filter is analogous, it is argued, to browsing by rabbits and other herbivores, which may subsist in winter upon a 3–5 year window of secondary-successional browse plants exposed above the snow in old burns. All spectra differ significantly from a white noise process at 10 11 years ($P < 0.001$). Spectra peak at 9 10 years for fire and 10 11 years for lynx.

in two separate pieces, 1919 1957 and 1958 1973. Otherwise, the downward and then upward trends spanning 39 and 14 years, respectively, are interpreted as a long cycle and add power to the spectrum at low frequencies, partially obscuring the 10-year peak.

Additional fire time series from the U.S., and monthly precipitation data from the U.S. and Canada, have been analyzed similarly. This work will be described elsewhere. There are 8 12 year periodicities in the U.S. fire data, although this is less pronounced than in Canada, owing partly to successful fire prevention. In northern Canada, minima in snowfall do not keep step with the lynx cycle, contrary to Watt's (1968, p. 155) preliminary observation, yet precipitation in some months does appear to be periodic. To the south of
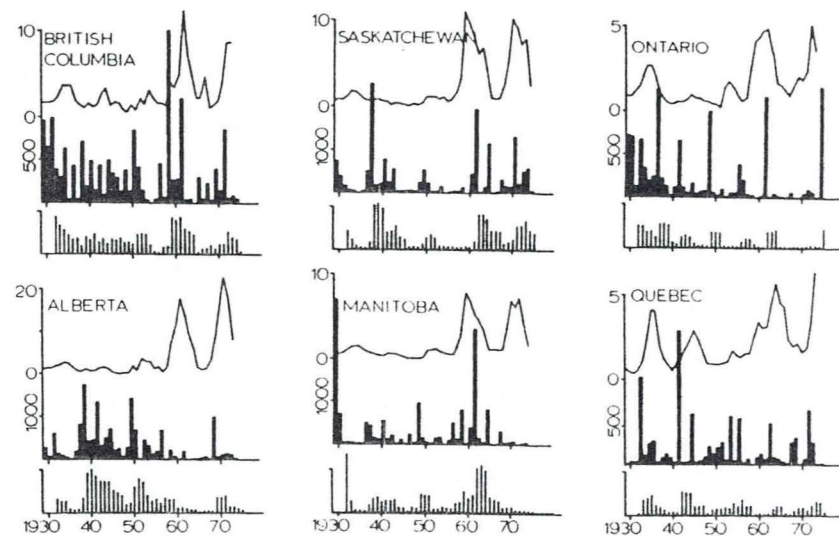
Fig. 4. Data for six Canadian provinces, 1919 1973, for lynx pelt harvests (*upper solid line*), total area burned annually (*middle histogram*, 1929 1973), and the 3-year moving average of area burned (*lower histogram*), which appears to be more quasi-periodic than the annual data. Scales are in thousands of pelts and thousands of acres burned. Full scale in the lower histogram is 1 million acres. Note the apparent disruption or cessation of the lynx cycle during 1929 1954, a continuation of an earlier decline trend begun about 1900 (Fig. 1). This appears to have been caused by over-exploitation of lynx rather than cessation of the snowshoe hare cycle (see 'Results')

Canada and in the U.S., spectra are much less or not at all periodic. Ten-year periods in precipitation have recently been determined for other parts of the world (King, 1973; Wood and Lovett, 1974), and these seem more convincing than before (Lamb, 1972), though the time series are still short.

Precipitation spectra are not at all as neatly periodic as forest fire spectra. This suggests that fire periodicity or quasi-periodicity arises from coincidences of hotter with dryer years. Such coincidences seem to explain tree-ring minima (Lyon, 1936; Diller, 1935; Fritts, 1962). This makes biological sense, because drought and fire weather depend not merely on gross precipitation, but on the deficit between precipitation and evapotranspiration.

Figure 4 presents the lynx pelt returns and area burned annually in the six largest Canadian provinces. The northern territories were omitted because fire data there begin only in 1947. The smaller Maritime Provinces contribute so little to the total lynx returns that they are superfluous, and animal migration from neighboring areas may influence their fur returns (Keith, 1963). There is a remarkable periodicity in area burned in Quebec and Ontario, and a rather weak periodicity in British Columbia and Alberta. This might correspond to the very imperfect periodicity also exhibited by lynx pelt returns in the past from British Columbia and as measured in the snowshoe hare questionnaire (Keith, 1963). Three- and four-year moving averages of area burned exhibit
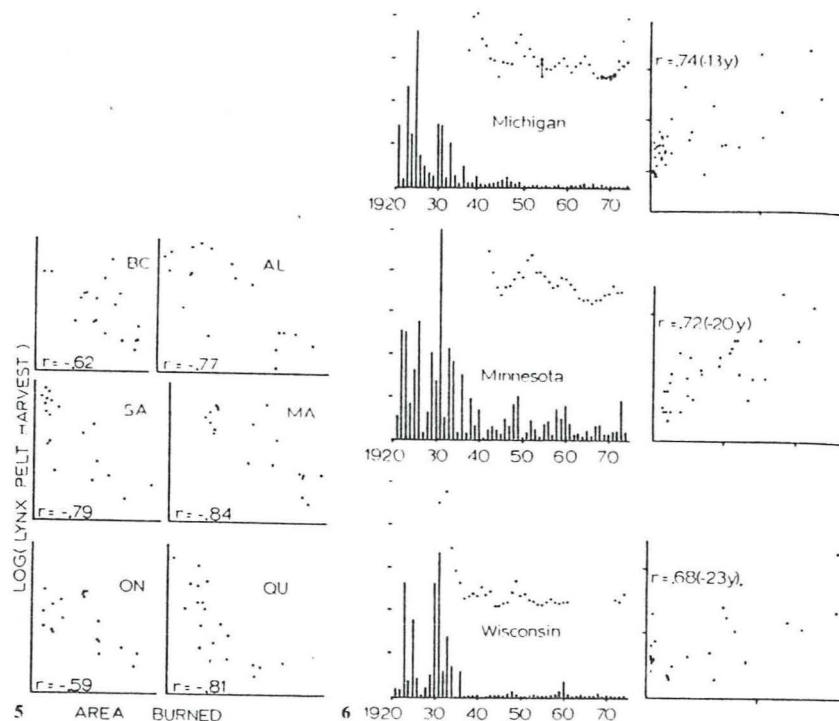
Fig. 5. Scatter plots of the logarithm of annual lynx pelt harvests (*ordinate*) versus the 3- or 4-year moving average of area burned (*abcissa*) for the same six Canadian provinces as in Figure 4. Data are for the latest 19 years (1955–1973) only, because of the interruption of the lynx cycle before that time, as discussed in the text. For $N = 19$, the 2-tailed critical values for correlation coefficients are $r = 0.575$ at $P = 0.01$, and $r = 0.693$ at $P = 0.001$. The time lag in years, between the leading (most recent) year of the 3–4 year average of area burned and the annual lynx pelt harvest which it predicts, is 16 (BC, British Columbia), 19 (AL, Alberta), 15 (SA, Saskatchewan), 17 (MA, Manitoba), 19 (ON, Ontario), and 15 (QU, Quebec). These are time lags for the maximum negative correlation; more details of lag-correlation patterns are shown in Table 1. A 3-year average of area burned is used in the three western provinces, and a 4-year average in the three eastern provinces, in accord with a trend toward higher correlations with the 3–4 year average in the west but a 4–5 year average in the east

Fig. 6. Area burned annually (1921–1974, *lower histogram*) and a snowshoe hare 'kill index' (*upper dots*) found by dividing the estimated snowshoe hare bag for the year by the number of small-game licenses sold, for the Lake states in the U.S. Scatter plots at right show the index (*ordinate*) versus the 3–4 year moving average of area burned (*abcissa*), with the correlation and the time lag in years previous (*in parentheses*). These are maximum correlations; see Table 2 for lag-correlation patterns. A positive correlation is caused by the common decline in both hare kill index and area burned over time. This common trend is important to the hypothesis that post-fire succession is largely controlling the hare and lynx cycles. A change in methods of estimation occurred in Michigan in 1954; a *vertical arrow* connects old and new estimates, made simultaneously in that year only. For 1968–1974 in Michigan, estimates become available for hunter-days spent in pursuit of snowshoe hares. Using hunter-days rather than small game licenses as the divisor of hare bags gives the index plotted as X's in the figure; this is ten times the license-index and is plotted at one tenth its value here. In Wisconsin, snowshoe hare bags were not available for 1962–1971

more apparent periodicity than do the annual data. This is biologically significant, since browsers are exposed to at least several years' accumulation of secondary-successional regrowth in any one year.

Figure 5 and Table 1 document the degree of correlation found in Figures 2 and 4, between area burned and lynx pelt returns, for the latest 19 years of data, 1955–1973. So far, precipitation data have been collected and analyzed for only three provinces and one state. Controlling for fire and precipitation does not significantly reduce the partial correlation of precipitation or fire, respectively, with lynx. The average effect is an increase in the partial coefficient, but the increase is more consistent for precipitation x lynx. This means that the residual effect not explained by fire tends to be explained by precipitation, but not so much vice-versa. This suggests the interpretation that forest fires are the primary controlling variable, and that precipitation modifies the response of hares to the abundance of post-fire successional habitat.

With the full (1929–1973) data set, the patterns of correlation with different time periods and lags are very similar to those for the latest 19 years in Table 1, but correlations are lower. This is caused by the 'lull' in the lynx cycle from 1930 to 1954 (Fig. 4). The 1955–1973 fluctuations account for most of the variance. Regression equations based upon the full data set consistently predict a lynx cycle over 1929–1954 where there was none. This is true for a variety of models involving three to four independent variables, including two fire and two precipitation lags. It seems clear that the 1929–1954 'lull' was not related to a similar lull in fires or precipitation. My guess is that the 'lull' was begun and maintained by overexploitation of lynx. Keith (1963, p. 115) reports that "...lynx have been practically extinct throughout most of south-central Alberta and Saskatchewan, and southern Manitoba for the past 25 years, yet the snowshoe hare cycle persists in this region. There are undoubtedly other places in Canada where the same situation holds." Butler (1942) discussed the problems of decline in lynx and other furbearers during this century. According to Butler (1942), in at least the western provinces of Canada, lynx had greatly decreased in numbers, especially relative to current numbers of the snowshoe hare, and current lynx peaks are about as high as former lows of the 1800's. Butler (1942) believed that lynx, at the time he wrote, were not being limited by food supplies but only by trapping pressures, and he demonstrated with a simple difference equation model that a trapper-lynx interaction could by itself have generated the cycles of 1919–1939 in Alberta. I find that his model not unexpectedly breaks down during the lynx upsurges of 1955–1973 if the lynx cycle has reasserted itself.

In Table 1, partial correlations are given between 'R' and 'F' but not between 'N' and 'F', for the following reason. Recall (Table 1, caption) that $N = \log(n(t-1))$ and that $R = \log[n(t)/n(t-1)]$. Then the following two regression equations are equivalent: (1) $\log[n(t)] = \log[n(t-1)] + f(P, F)$ and (2) $\log[n(t)/n(t-1)] = \log[n(t)] - \log[n(t-1)] = f(P, F)$. In designing regression equations to predict $N = \log[n(t)]$, $\log[n(t-1)]$ always enters the equation first; because of the large range of variation in lynx pelt numbers, $n(t)$ is always highly-correlated with $n(t-1)$. Once $\log[n(t-1)]$ has entered the equation to predict N, the residuals are then identical to those for R, and so the correlation of further independent variables (P, F) with R and not with N is wanted for selection

Table 1. Simple and partial correlation coefficients between the lynx pelt cycle and forest fires and precipitation. Dependent variables are represented symbolically by N, for the logarithm of the annual lynx pelt harvest, and by R, for the logarithm of the annual 'rate of increase' in the lynx pelt harvest. Independent variables are symbolized by F, for area burned, and P, for precipitation. Maximum and minimum correlations with area burned (F) appear at various times in the past. Hence, along any row, the peak correlations with fire are given at four different time lags, along with the time lag (in parentheses) at which the maximum or minimum appears. The F-variable was a 4-year moving average; hence, a time lag of (5) refers to the sum of area burned 5, 6, 7, and 8 years previous. In Alberta, then, $N \times F$ refers to the correlations of N with area burned (F); reading across this row, there was a minimum value of $r = 0.73$ found at lag 14, i.e., with the sum of area burned at 14, 15, 16, plus 17 years previous. 'Partial $R \times F(P)$' refers to the partial correlations of R with area burned, controlling for the precipitation variable for which the simple correlation ($R \times P$) is also given. $R \times P$ was chosen because it had the maximum absolute value among precipitation variables tested. For partials, the time lag at which a maximum or minimum value occurs may differ by ± 1 year from the simple correlations. 'Partial $R \times P(F)$' refers to the partial correlation with the same precipitation variable as in $R \times P$, controlling for various fire (F) variables, whose time lag is given in parentheses. All these correlations, for Canada, are based upon the latest 19 years (1955–1973) of data, as explained in the Results. Hence, two-tailed significance levels are $r = 0.456$ for $P = 0.05$; $r = 0.575$ for $P = 0.01$; and $r = 0.693$ for $P = 0.001$. For the partials, with 3 fewer d.f., increase these critical r values by 0.05

Alberta					
$N \times F$		−0.53(5)	−0.01(9)	−0.73(14)	0.69(19)
$R \times F$		−0.27(4)	0.28(8)	−0.41(12)	0.64(17)
Partial $R \times F(P)$		−0.25(4)	0.26(7)	−0.41(14)	0.64(18)
$R \times P^*$	−0.69				
Partial $R \times P(F)$		−0.69(4)	−0.71(7)	−0.70(14)	−0.69(18)
Saskatchewan					
$N \times F$		−0.39(2)	0.60(7)	−0.79(13)	0.42(20)
$R \times F$		−0.46(0)	0.41(4)	−0.66(11)	0.54(18)
Partial $R \times F(P)$		−0.86(0)	0.38(5)	−0.57(12)	0.59(17)
$R \times P$	−0.39				
Partial $R \times P(F)$		−0.77(0)	−0.36(5)	−0.02(12)	−0.62(17)
Ontario					
$N \times F$		−0.62(5)	0.52(10)	−0.59(17)	0.18(21)
$R \times F$		−0.33(2)	0.47(7)	−0.33(15)	0.49(20)
Partial $R \times F(P)$		−0.31(3)	0.51(8)	−0.39(12)	0.63(21)
$R \times P$	−0.44				
Partial $R \times P(F)$		−0.43(3)	−0.48(8)	−0.48(12)	−0.60(21)
British Columbia					
$N \times F$		−0.68(6)	0.52(12)	−0.60(17)	0.33(20)
$R \times F$		−0.49(4)	0.45(10)	−0.35(16)	0.34(19)
Manitoba					
$N \times F$		−0.35(2)	0.46(9)	−0.84(15)	0.88(20)
$R \times F$		−0.29(2)	0.39(6)	−0.63(13)	0.73(18)
Quebec					
$N \times F$		−0.38(2)	0.61(9)	−0.81(13)	0.44(18)
$R \times F$		−0.07(4)	0.39(7)	−0.55(11)	0.38(14)
Canada[b]					
$N \times F$		−0.59(4)	0.66(9)	−0.83(14)	0.59(20)
$R \times F$		−0.60(1)	0.66(7)	−0.55(11)	0.59(18)

[a] Precipitation variables: Edmonton, Alberta — the sum of Dec.–Feb. precipitation for the same winter as lynx trapping plus two previous winters; Prince Albert, Saskatchewan — the sum for Nov.–Mar. for the winter of lynx trapping; Mooseonee, Ontario — as for Alberta

[b] Using the sum of lynx pelt harvests and area burned for the above six provinces

of additional variables. Note, however, that this is a pragmatic consideration, and that fire (F) is often more highly correlated with N than with R, as is discussed later.

The partial correlations in Table 1 indicate that at least 50% of the variance in lynx pelt returns can be predicted by one precipitation variable plus one fire lag combined. The addition of a second fire lag and/or a second precipitation lag can bring the multiple R^2 up to 70% or more. Full details of these regression analyses will be presented elsewhere. Some general results, not documented here, are as follows: Precipitation in May-June and May-July, coinciding with some of the 'best' correlations of Meslow and Keith (1971), gave lower correlations with lynx pelt numbers than did precipitation in November-March and December-February, chosen because of Watt's (1968, 1973) preliminary work. Maximum correlations and the most regular patterns of increase and decrease of correlation with time lag occurred with 3–5 year moving averages of area burned. Correlations tended to be greater with 3–4 year moving averages for the three western provinces and with 4–5 year averages for the three eastern provinces. For partial fire-lynx correlations, controlling for any precipitation variable, the time lag of a maximum or minimum correlation either did not change or was shifted by ± 1 year relative to the simple correlation, and the pattern of increase and decrease with lag persisted, essentially unchanged in magnitude. There was less stability in the partial lynx-precipitation correlations. The calendar period or the sum (1–3 years) most highly correlated might change rather unpredictably relative to the simple correlation with a change of controlling fire variable. Maximum correlations were typically much lower ($r = -0.3$ to -0.4) than the maximum given in Table 1. These considerations also lead me to believe that precipitation is a modifying but not primary variable in predicting hare and lynx catch.

The estimated snowshoe hare bag in the Lake States has been successfully related to forest fires and precipitation (Table 2, Fig. 6), in spite of the crudeness of these forms of estimate (Keith, 1963, p. 12). Correlations between snowshoe hare kill indices and area burned were always positive, but peaked at certain lags (Table 2). A downward trend in both of these variables, evident in Figure 6, leads to these high positive correlations. This is expected if hare populations are proportional to the area of successional habitat. Next, the common trend owing to temporal decline (forest fire suppression) was removed by partial correlation and regression. The partial correlations between area burned and the hare kill index, controlling for temporal trend, bring out strong negative correlations just as seen for fire and lynx in Canada (Table 2).

The last 13 years of data in Minnesota were treated separately (Table 2, bottom) in order to explore two notions, (1) that the suppression of fires might uncouple the fire-rabbit connection and (2) that with suppression of fires, precipitation will assume more importance. The first notion is rejected, since area burned is still highly correlated with hare kill. In Michigan, correlations for the last 14 years of record exhibit maximum values of −0.77(−2 year), +0.51(−16 year), and −0.71(−21 year) between lynx numbers 'N' and area burned (three year moving average). The pattern is different but values are not lower than previously. The second notion is borne out because precipitation is more highly correlated with hares in Minnesota in later years (Table 2).

Table 2. Simple and partial correlation coefficients between the snowshoe hare kill index and forest fires and precipitation, in the United States. The scheme is the same as in Table 1, but N represents the logarithm of the annual hare kill index, and R represents the 'rate of increase' in this index. The variable F is the three year average of area burned, at the time lag in years previous shown in parentheses. Correlations at some long lags have been omitted where a maximum or minimum might exist but the correlations are not large, in the right of the table. Two-tailed significance levels are given as *(0.05), **(0.01), and ***(0.001). For Minnesota, 1960-1973, the precipitation variable used in the partials $R \times F(P)$ was the maximum negative one, $r = -0.59$. Although negative correlations between snowfall and hares are expected and have been the rule in lynx and hare analyses, the highest correlation in this case is positive (lowest line, $r = +0.85$)

Michigan					
$N \times F$	0.69(6)***	0.40(9)*	0.67(13)***	0.19(18)	
Partial $N \times F$(Time)[a]	0.42(6)**	-0.21(9)	0.32(13)	-0.73(18)***	
$R \times F$	0.15(4)	-0.25(8)	0.15(12)	-0.31(16)	0.23(21)
Partial $R \times F$(Time)	0.27(4)	-0.30(8)	0.31(12)	-0.42(16)*	0.46(21)*
Wisconsin					
$N \times F$	0.29(5)	0.49(7)**	-0.13(12)	0.62(16)***	-0.39(21)*
Partial $N \times F$(Time)	-0.07(5)	0.16(8)	-0.85(12)***	0.38(16)*	-0.83(19)***
$R \times F$	-0.32(3)	0.03(7)	-0.39(11)*	0.35(15)	-0.47(18)**
Partial $R \times F$(Time)	-0.24(3)	0.24(7)	-0.31(11)	0.71(15)***	-0.42(18)*
Minnesota					
$N \times F$	0.03(4)	0.34(10)	0.16(13)	0.68(19)***	
Partial $N \times F$(Time)	-0.70(4)***	-0.24(10)	-0.60(13)***	0.39(19)*	
$R \times F$	-0.59(4)**	-0.32(11)	0.18(14)	-0.43(21)*	
Partial $R \times F$ Time	-0.69(4)***	-0.33(11)	0.46(14)*	0.03(21)	
Partial $R \times F$(P)	-0.74(4)***	-0.32(11)	0.23(14)		
$R \times P$[b] +0.47					
Partial $R \times P$(F)	-0.16(5)	-0.14(12)	-0.14(15)		
Minnesota 1960-1973					
$N \times F$	-0.87(5)***	0.88(10)***	-0.80(16)***	0.89(21)***	
Partial $N \times F$(P)	-0.81(5)**	0.86(10)**	-0.67(16)*	0.90(21)***	
$N \times P$[b] -0.59*					
Partial $N \times P$(F)	0.45(5)	-0.41(10)	0.80(16)**	-0.36(21)	
$R \times F$	-0.70(2)*	0.77(8)*	-0.64(13)	0.69(19)*	
Partial $R \times F$(P)	-0.29(2)	0.57(8)	-0.60(12)	0.47(20)	
$R \times P$ +0.85**					
Partial $R \times P$(F)	0.70(2)*	0.73(8)*	0.74(13)*	0.73(19)*	

[a]   The effect of a temporal downward trend in both variables was removed by partial correlation
[b]   Precipitation variables: Minneapolis, Minnesota – (1) for the full time period, the sum of precipitation for Dec.-Feb., the same winter as snowshoe hare kill estimates; (2) for the 1960-1974 time period, for N: the sum for Dec.-Feb. for the winter of harvest plus two previous winters; (3) 1960-74, for R: the sum for Nov.-Mar. for the winter of harvest plus two previous winters

and the partials show that fire and precipitation are both informative predictors of hare kill. I suggest this interpretation: as the magnitude of fluctuation in area burned has decreased, so too, in direct consequence has the magnitude of hare fluctuations; the absolute magnitude of hare fluctuations accounted for by precipitation may not have changed, but this currently amounts to a larger proportion of the variance in hare population change. Unfortunately, we lack data for a number of recent years in Wisconsin, the state in which fire suppression has been greatest.

Discussion

It remains to review the quality of the evidence and to interpret it biologically. The historical fire data in Figure 1 are naturally of low precision; yet these data are important because more accurate forest fire data begin only as recently as 1929 in Canada. Correspondence between the lynx pelt cycle and the forest fire record in Figure 1 could have been much worse than it appears, and indeed might have discouraged any belief in a fire-lynx connection in the past. Yet these data reinforce the correlation studies of more recent data by exhibiting similar coincidences in periodicity and phase between fire and lynx. It is the quality of the data and their geographical distribution which probably account for particular non-correspondences with the lynx cycle.

The correlation analyses (Fig. 5, Tables 1 and 2) provide the most convincing evidence for a connection between the lynx cycle and independent, environmental variables. In spite of the large number of coefficients tested (lags 0-23 and moving averages 1-5, or 120 coefficients in each province), levels of significance are high for the peak correlations, and a greater number of correlations have been found at a given level of significance than expected if no correlation exists. What is more important, there is a consistent pattern in the time lag for maximum and minimum correlations in different provinces and states. Part of this common pattern may be attributed to continent-wide syncrony in peak fire years, but there also exists some asyncrony, especially from east to west and north to south. Butler (1953) pointed out that peaks of fur-bearer cycles occur earliest in central Canada (Athabasca Basin) and 1-2 years later to the east and west. A similar patterns occurs in the area burned (Fig. 4). Examining the leading years of peaks in the moving average of area burned (Fig. 4), circa 1940, 1950, 1960, and 1970 the peaks occur later in Quebec (4/4 peaks) and British Columbia (3/4) than in Saskatchewan and Manitoba (which march together), while peaks may occur later, the same year, or in one case earlier, in Ontario and Alberta than in the two central provinces.

The concomitant decline in both hare kill and area burned in the Lake States (Fig. 6), seen also for ruffed grouse (Gullion, 1966, 1970; Sharp, 1963), is a convincing piece of evidence suggesting that forest fires at least set the upper limits to hare (and lynx) population.

At the same time, spectral analysis and the positive-negative oscillation of correlation coefficients with time lag strongly suggest that hare-lynx *periodicity* is also caused by a periodicity in fire occurrence. Area burned has also declined in Canada, but not as recently or as rapidly as in the U.S., and the 1900-1954 lynx decline of Figure 1 is probably owed to overexploitation of lynx rather than to snowshoe hare decline, as discussed above.

Another important piece of evidence is the time lag pattern of maximum positive and negative correlations between lynx and area burned (Tables 1 and 2) appearing at biologically reasonable time lags for post-fire secondary succes-

an external forcing function as causes of the hare-lynx cycle is to prevent second-
ary succession (i.e., fire) over so large an area that immigration is negligible.
The U.S. Forest Service appears to have done the experiment, in the Lake
States (Fig. 6). Formerly, snowshoe hares appeared to follow an 8–10 year cycle
in the Lake States (Keith, 1963; Fig. 6). More recently, since 1950, hare fluctua-
tions have been severely damped and their periodicity, if it exists, is more
disturbed. Minnesota, with a fire record which is still periodic, also appears
to exhibit a continuing 10-year hare cycle of low amplitude. In Michigan, the
cycle appears to have been broken in 1950–1960 but perhaps to have resumed
in 1960–1970. In Wisconsin, where fires have been most radically suppressed,
fluctuations appear to have been stopped, however, the fire time series may
still contain a weak 10-year signal which may just be reflected in the hare
kill index. Damping of the hare cycle in the Lake States could also be attributed
to subdivision of habitat owed to land development, according to Dolbeer
and Clark's (1975) hypothesis. However, correlations in recent years (Table 2)
indicate that fires are still important in hare trends.

The snowshoe hare-Canada lynx cycle, because of its astonishing regularity,
has long provided an unequaled example for theoretical ecologists when they
assert that limit cycles may occur in ecological systems. This study may now
provide ammunition to those who wish to deny the possibility of limit cycles
in nature, or the importance of theoretical ecology in general. It is worth pointing
out, then, that either periodic or aperiodic environmental fluctuations can induce
limit cycle behavior in systems otherwise converging upon a point equilibrium
(May, 1974). It would not be surprising if there resulted high correlations be-
tween these environmental disturbances and the system's state, e.g., lynx abun-
dance or rate of increase. Furthermore, I have not *disproven* the existence of
a limit cycle in the lynx-hare system, and I am ill-equipped to state sufficient
conditions for doing so. The disproof proposed above, suppression of fires
in the Lake States, reveals ambiguous results, and might still be interpreted
in favor of a limit cycle in view of May's (1974) discussion.

If coincidence in periodicity could be relied upon, lynx cycles should be
explained by sunspots, which exhibit a very neat 10–11 year peak in their
variance spectrum. Sunspots and lynx time series marched in phase and ampli-
tude for a string of years, about as long as our fire time series; now the
two are completely opposite in phase (Moran, 1949). A regression analysis
limited to either the in-phase or out-of-phase periods of the sunspot record
would probably yield very high correlations between sunspots and lynx. The
moral is that neither coincidence in periodicity nor the proportion of variance
explained by a regression model provide an ultimate test of any proposed cause
of the lynx-hare cycle. We must know whether dependent and proposed explana-
tory variables are directly related by intervening biological mechanisms. The
quantitative effects of these mechanisms in linking game cycles with some pro-
posed cause must be demonstrated by observation and experiment in the field.
The main significance of demonstrating periodicity in fire and weather data
is that it gives us good cause to suspect the hare-lynx cycle and other game
cycles of being 'forced oscillations' driven by environmental fluctuations. Here-
tofore there has been no convincing evidence in favor of 'forced oscillations',

and the idea of limit cycles has dominated the ecological stage. I believe that
the cautions expressed in these last two paragraphs cannot be overemphasized,
but neither should they be used to prevent the advancement of plausible compet-
ing explanations such as those proposed here.

Rabbit Food: Boreal Forest Succession

It is now important to review the biological and historical evidence that increases
in land area undergoing secondary succession can directly cause increased
growth, survival, and reproduction of snowshoe hares or other wildlife species
possessing similar food and habitat requirements. Although there exist readily
acceptable, plausible mechanisms connecting weather with survival and repro-
duction of wildlife species and domestic (open-range) livestock, forest fires *qua*
boreal forest secondary succession present a relatively novel mechanism for
wildlife population fluctuation, one for which the evidence has not been ad-
equately reviewed and which has been only superficially appreciated by most
(non-wildlife) ecologists. The evidence falls naturally into two arguments. First,
the preferred foods of snowshoe hares and many other 'secondary-successional'
wildlife species are precisely those plants which increase during post-fire succes-
sion; preference implies greater nutritional value, and so implies the potential
for greater carrying capacity and for population increase. Second, there are
numerous case-histories of post-logging or post-fire population increases of
wildlife species possessing secondary-successional browse plant preferences.

Successional habitat types are inferred by game managers to hold a greater
quantity and/or quality of both summer forage and winter browse for many
species, and to be a vital tool for managing the 'secondary-successional' game
species (Dasmann, 1964; Klein, 1970; Heinselman, 1973; Viereck, 1973; Rowe
and Scotter, 1973; Johnsgard, 1973). Many game animals like deer, moose,
elk, and ruffed and sharp-tailed grouse conspicuously seek out and forage within
successional habitat types if these are not over-browsed (ibid.).

There is substantial agreement in browse preference among the 'successional'
wildlife species of the boreal forest. This is surely more than coincidence, and
probably reflects the relative value of successional food plants to these species.
A handful of studies have documented the high overlap in winter browse foods
and habitat use among snowshoe hares, white-tailed deer, and moose (Dodds,
1960; Bookhout, 1965; Telfer, 1972, 1974). The order of preference of snowshoe
hares for winter browse is fairly clear and geographically repeatable: (1) willow,
aspen, birch, hazel, and a number of other deciduous, second-growth woody
plant species; (2) white cedar; (3) pines; (4) firs; (5) spruces (Aldous and Aldous,
1944; Aldous, 1936; Baker et al., 1921; Bider, 1961; Bookhout, 1965; Cook
and Robeson, 1945; Dodds, 1960; Grange, 1932; Harper, 1932; Seton, 1953;
Telfer, 1972). This follows a successional sequence, with the exception that
jack pine and white spruce may be the first trees to occupy certain edaphic
sites, and that white cedar is out of place. White cedar is relatively rare over
large areas, is edaphically restricted, but is still probably a very palatable alterna-
tive food.

Deer, especially white-tailed deer, and moose follow much the same sequence of browse preference and habitat-type selection (ibid., and Aldous and Smith, 1938; Cowan, 1945; Cowan et al., 1950; Crête and Bédard, 1975; Dasmann, 1964; Dills, 1970; Heinselman, 1973; Irwin, 1975; Klein, 1970; Lawrence and Biswell, 1972; Leege and Fultz, 1972; LeResche and Davis, 1973; Lyon, 1969; McCaffery et al., 1974; Mueggler, 1966; Nixon et al., 1970; Phillips et al., 1973; Skinner and Telfer, 1974; Spencer and Hakala, 1964; Stevens, 1970; Wallmo et al., 1972; Wetzel et al., 1975). Despite the variability of these reports, they confirm a strong tendency toward secondary-successional food and habitat types on the part of deer and moose. In many places, the later-successional conifers, especially white cedar and balsam fir, are by far the most abundant browse and constitute a large part of the winter diet of hares, deer, and moose. However, in the studies cited above, the ratio of use (browsing) to availability or twig abundance is always relatively low for the conifers and relatively high for many of the species of deciduous browse plants. The conifers contain terpenes and other compounds which inhibit rumen microbial function in ungulates (Oh et al., 1968), making conifer needles relatively unpalatable even though they are an abundant source of maintenance energy in winter. Caecal digestion in rabbits possibly is also interfered with by conifer toxins.

Grouse are remarkably limited in their preferred winter foods, ruffed grouse to the staminate-catkin winter buds of aspen, and sharp-tailed grouse to birch buds where these are available (Doerr et al., 1974; Ellison, 1975; Gullion, 1966, 1970; Hamerstrom, 1963; Johnsgard, 1973; Korschgen, 1966; Robinson, 1969; Rusch and Keith, 1971; Sharp, 1963; Svoboda and Gullion, 1972; Weeden and Ellison, 1968). The geographic range of the ruffed grouse coincides remarkably well with what has been defined as the range of aspen and birch (Johnsgard, 1973; Svoboda and Gullion, 1972). Exactly the same statement could be made for snowshoe hares, and moreover, aspen and birch could be said to define the range of boreal forest secondary succession. For most herbivorous birds and mammals in the boreal forest, the main and preferred habitats and food types are secondary-successional ones.

In summer, snowshoe hares (ibid.), and deer and moose (ibid.) eat a wide variety of succulent green plants and berries. Herbage within reach of a rabbit is in very short supply in a late-successional or climax forest but is superabundant soon after fire or logging (Viereck, 1973; Heinselman, 1973; Irwin, 1975; Wallmo et al., 1972; Dasmann, 1964; McCaffery et al., 1974). Deer, moose, and ruffed grouse seek out these early-successional plant foods and habitat types for heavy summer utilization (ibid.). It is not necessary to argue whether summer or winter foods limit herbivore populations, because post-fire successional habitats contain more of both summer and winter foods of the 'successional' wildlife species.

The agreement in food and habitat preference of rabbits, moose, deer, and ruffed grouse, combined with the known ability of herbivores to discriminate among food plants of different nutritional values, constitutes *prima facie* evidence that the preferred successional habitats and foods can increase herbivore populations if the plants become more abundant. This does not deny that some animals (e.g., sage grouse, spruce grouse) are adapted and highly special-

ized to use some plants which are especially unpalatable and toxic to many other animals. I will also cite, in passing, from the abundant evidence that herbivorous mammals are able to select from among different plant species and different individual plants those which tend to decrease their intake of toxins and digestibility-reducing chemicals, and to increase their nutrient intake (*ungulates*: Cowan et al., 1950; Dasmann, 1964; Einarsen, 1946; Klein, 1970; Longhurst et al., 1968; Radwan and Crouch, 1974; Torgerson and Pfander, 1971; Ward, 1971; *mammals*: Freeland and Janzen, 1974; Levin, 1976; *European hares*: Lindlof et al., 1974; Miller, 1968; Miller and Watson, 1974). There is limited evidence that preferred plant species not only contain more useable nutrients, but also result in greater weight gains, fertility, mating success, and better health in wild animals (Klein, 1970; Dasmann, 1964; Verme, 1969). This is, of course, a well-established fact for domestic animals and range livestock, but the evidence for wild animals is scanty.

The second theme is that episodes of secondary succession following in the wake of logging and fires have caused long-term increases and finally, when succession is completed, decreases in vertebrate herbivore populations. Most of these changes in game abundance date from the past 30–80 years and are not related to any 'cycles'; instead they parallel the history of logging and fire protection in the U.S.

Decline in deer (McCaffery et al., 1974; Nixon et al., 1970; Wetzel et al., 1975) and in moose (Phillips et al., 1973) populations in Minnesota, Wisconsin and Ohio in the past 30 years is attributed to a reduction in the area burned or lumbered, and simultaneous maturation of areas logged or burned in 1870–1920. An increase in moose numbers and fecundity in northwest Minnesota was connected with a recent forest fire (Phillips et al., 1973). The historical rise and decline of deer in the Arkansas Ozarks (Halls and Crawford, 1960) is attributed to fires and logging early in this century, followed by maturation of the forest and a reduction in quality and mainly quantity of both winter and summer foods. The high deer populations of Pennsylvania are attributed to logging and burning in the 1930's (Marquis, 1973). Forest fires of 1890–1911 greatly increased deer, moose, and elk habitat in Idaho and Montana, but carrying-capacity has gradually declined as secondary succession proceeds (Leege and Fultz, 1972; Lyon, 1969; Mueggler, 1966). Several episodes of deer increase after lumbering and fires, followed by plant succession and finally a population 'crash', usually during a hard winter, are given by Stanton (1963) for Maine. Increase in the Alaskan Kenai moose herd is attributed to a 1947 fire by Spencer and Hakala (1964). Edwards (1954) documented increases in small mammals, moose and deer, and decreases in woodland caribou, after a large fire in Wells Gray Provincial Park, British Columbia. Leopold (1950) reviews evidence mainly for California showing how deer have responded to plant succession. Ruffed grouse in Minnesota (Gullion, 1966; Marshall, 1954) and Pennsylvania (Sharp, 1963) have declined as the aspen stands created by fire and logging early in this century matured. Gullion (1970) obtained a high correlation between area burned and the size of grouse population indices for Minnesota.

All of this evidence is apropos snowshoe hare response to plant succession, because of the high overlap in food and habitat preferences between moose,

deer, ruffed grouse, and snowshoe hares, cited above. Almost invariably, the literature accounts for short-term game population trends by weather or other changes while invoking long-term trends in secondary succession or in habitat quality to explain long-term trends in populations. There have, however, been two convincing papers relating snow depth to long-term population trends. Gilbert et al. (1970) discuss deer die-offs in winter, relating these to deep snows; full recovery of the population could require several years for deer, so this is at an intermediate time scale. Edwards (1956) attempted to relate long-term (mean) trends in snow depth to ungulate populations in the northern Rocky Mountains, but a quantitative analysis is lacking.

In conclusion, in the boreal forest of North America, successional habitats contain the most palatable, most preferred, and probably the most nutritious (relative to the animals' adaptations) plant foods and by far the greatest amount of both winter and summer foods within reach of ungulates and especially snowshoe hares. There have been numerous historical episodes of widespread lumbering and fires, followed by population increases of deer, moose, elk, and ruffed grouse, or, declines of these species have followed the course of forest maturation. The food and habitat preference of snowshoe hares suggests that they should similarly 'track' the course of post-fire plant succession. I have further shown that (1) fire exhibits a 10-year periodicity over huge areas in Canada, and that (2) lynx and hare kill is highly correlated with area burned, at a time lag in the past appropriate to secondary succession, and in a time window (3–5 years) appropriate to snowshoe hare utilization of successional vegetation. I have also shown that snowfall is strongly implicated in lynx and hare population trends, perhaps by modifying secondary-successional browse availability as well as influencing energy demands of the animals.

In seeking an explanation of 10-year furbearer cycles, we want to establish causes which have accounted for large and sustained population increases and decreases over long periods. By this criterion, ecological and historical evidence makes post-fire secondary succession the best-supported mechanism yet proposed to account for the snowshoe hare-Canada lynx pelt cycles. I hasten to add that this is still only a hypothesis, fortunately one which can be tested in a number of ways, and which might yet be disproven.

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Contents

Office Memorandum

TO   :   Don Childress, Glenn Erickson   DATE: 8-6-90
            & Tom Hintz

FROM :   Howard Hash

SUBJECT: Lynx Report

Enclosed are copies of the lynx report as requested. A long search reveals that very little detailed information is available on the effects of various levels of harvest, prey base threshold levels required to activate population increases and decreases and what factors enable a lynx population to exist in marginal habitats such as Montana.

Hopefully it will provide a somewhat better understanding of lynx biology and some explanation of the general lynx situation, thus assisting with the decision making process for 1990-91 seasons and regulations, which will be a topic at the August 9-10 managers' meeting.

HH/vm
Enc.
cc: Rich Clough
     John Firebaugh
     Jim Cross
     Bruce Campbell
     John Cada
     Mike Frisina
     Graham Taylor
     Charlie Eustace
     Harold Wentland
     Neil Martin

MONTANA LYNX POPULATION STATUS AND CONSIDERATIONS (1990)

INTRODUCTION

The purpose of this report is to describe basic lynx
biology and the current Canada Lynx population status based
on an extensive literature review, Montana harvest data,
research results, correspondence with neighboring states and
provinces and direct contact with acknowledged lynx
authorities, Montana wildlife biologists, wardens, trappers
and fur buyers. Associated information is presented as an
aid in setting harvest season and establishing regulations.

The most appropriate recommendations regarding the 1990
- 1991 lynx trapping season, quotas and trapper limits must
be formulated and presented to the commission at mid- August
meeting.

BACKGROUND

The lynx is Holartic in distribution, ranging across
the boreal forests of North America and Eurasia. They are
present across nearly all of Canada and Alaska with a
secondary range extention down the Rocky Mountains that has
receded Northward somewhat during the past 100 years. The
best lynx habitat and population in the Northwestern U. S.
are found in Montana.

The lynx is an animal of the homogeneous boreal forest
that is primarily composed of spruce, fir, aspen,
cottonwood, willow, and alder with many bogs, lakes and
thickets. They are not well adapted to other habitats and
show very limited ecological amplitude in adapting to other

habitats . There are periodic reports of dispersal
southward into other habitats and settlements, and north
onto the tundra, but these movements are ephimeral and occur
because of periodic collapses of snowshoe hare populations
in the core range (Banfield 1974, Mech 1980). Lynx also
exhibit long distance movements during peak population
levels from core ranges to areas of marginal habitat. The
lynx is extremely closely tied to its primary prey species,
the snowshoe hare, and apparently has a very limited ability
to switch or adapt to other prey when hare numbers are down.
Only hares can support high density lynx populations (Brandt
and Keith 1979). Invariably, lynx populations decline
significantly following declining hare populations. Lynx
habitat must support good snowshoe hare populations. Hare
populations are known to fluctuate on approximate 10 - year
cycles in the northern boreal forest, which is caused by the
interaction of the snowshoe hare with its food supply. Hare
populations can reach astounding abundance; densities of
about 4400 hares per square mile have been recorded (Brandt
et al 1976). As hare populations peak for a given area
they begin to overbrowse their range and the quality and
quantity of the food supply becomes the limiting factor.
When heavily browsed some woody plants produce secondary
compounds including terpenes, which inhibit the digestion of
protein by certain herbivores. As hares began to
over-utilize their range they are affected by a declining
food supply both in terms of quantity and nutritional value
(Brandt 1981. Brandt et al 1985).

The initial decline in the hare densities is likely the result of direct winter starvation, followed by several years when continued malnutrition, predation and low reproductive capability combine to depress populations. During this period the browse is starting to recover however, continued predation alone is believed to depress hare numbers during the final stages of the decline.

As hare populations decline, lynx cannot find an adequate alternate food source and their numbers also begin to decline. A sudden drop in the production and survival of the young is more the cause of lynx declines than is direct starvation of the adult populations. Recruitment virtually ceases at the low point in hare availability and nontrapping mortality of kittens during population declines approached · 100%. Lynx fecundity is closely correlated with food availability and relative nutritional planes. Hare flesh is very high in protein. The lynx cycle normally lags about one year behind the hare cycle. The lynx's dependence on a single food base is unique among furbearers. This cycle covers most of the boreal forests in a somewhat synchronous fashion and the severity of population crashes for hares and lynx is somewhat variable. It is likely that the intensity or actual lowest population level of each preceding hare and lynx decline directly affects the peak population levels of both species during the succeeding cycle. Variable climatic and vegetative conditions also affect the amplitude and duration of the cycle. No two population cycles are the same.

It is readily apparent that the Montana lynx picture is much different than the classic Canadian situation previously described. There is very little similarity between the basic habitats. Our lynx range throughout the primary Rocky Mountains and their associated valleys where the best snowshoe hare densities occur in association with lodgepole pine and/or subalpine fir stands with shrubby understory, openings or ecotonal areas. These areas are seldom in large scope. There are no records or other information available that indicates Montana hare and lynx numbers have ever approached population levels even remotely comparable to those produces in the boreal forests, presumable because of the limited snowshoe hare habitat that precludes large scale population irruptions. Hare numbers in Montana appear to vary on the order of from a few individuals to perhaps a few dozen per square mile in the best of habitats. Hare numbers in the boreal forests vary from a low of a few dozen per square mile up to 4,000 + per square mile.

All available information indicates that Montana lynx are somehow related to and affected by Canadian populations. There are several documented instances of relatively straight - line, long distance movements by lynx that could place Canadian animals in Montana and Montana lynx into Canada. Specifically, two radio - collared lynx made direct movements of 90 and 125 miles within Montana and into Canada, respectively. These animals were radio collared

during the mid 1980's in conjunction with bobcat research. Mech (1980) worked with lynx extensively in northern Minnesota and found that lynx exhibited very large home ranges of up to about 200 square miles and one animal dispersed 377 miles over a period of 807 days from Minnesota to Ontario. Saunders (1963b) and Nellis and Wetmore (1969) also recorded long range movements. It appears that large home range utilization and long linear movements are primarily associated with high lynx numbers and the need for dispersal to alleviate crowding and social stress. Some authors have suggested long range travels may also occur when hare populations crash, causing lynx to desperately search for another food source. It follows that certainly adequate long range movements could occur to permit the stocking of Montana habitats from the core Canadian ranges when required conditions develope. It is likely that any significant dispersal could only occur in unison with unusually high populations of hare and lynx, which does not occur with every 10 year cycle. Sample sizes have been very small and confidence levels are unknown; however, enough reliable information exists to confirm population exchange and to suggest an explanation for Montana lynx population variations.

Once Montana habitats receive a periodic stocking they may be able to further increase to the apparent high levels present during the 1972 - 1976 period. Local hare populations, trapping pressure, climatic conditions and

other unknown factors likely combine to determine the
amplitude and duration of the population cycle.

Personal discussions with Dr, Gary Koehler, probably
the most experienced lynx researcher, Dr, Bart o'Gara, noted
wildlife and lynx authority, Dr. Ted Bailey, Alaska
biologist, Canadian wildlife biologists and leading lynx
trappers tend to support this general view of the lynx
phenomenon. Certainly, there is no conclusive, quantifiable
information available to explain the situation or to
enumerate a threshold number of animals that must disperse
or what level of hare population must be present to cause
population gains or losses in Montana.

It is generally agreed that no amount of normal
trapping pressure can influence lynx numbers during the
higher portions of a Canadian cycle and that any trapping
pressure may be directly addative to mortality when
population numbers are at the lowest point, especially in
marginal habitat such as Montana.

HARVEST DATA

Harvest data from previous years is utilized
substantially as valid information in wildlife management
during the process of setting seasons and regulations for
future harvest despite the fact that it is generally
considered suspect unless there are other forms of
information available to verify the general situation. It
would be entirely possible to harvest the last animal from a

given population using only the harvest data from the previous year.

Lynx harvest data for Canada are available from fur company returns for the period 1735 - 1950. An average of about 15,000 lynx pelts were marketed in Canada during the period 1920 - 1960 with ten year peaks averaging approximately 25,000. Since 1960, an average of about 35,000 pelts per year, and ten year peaks averaging around 55,000 animals. Recent peaks have occurred during 1961-62, 1972-73, and 1980-83.

Montana lynx harvest data is much less definitive. Some records exist prior to 1972; however, reasonably reliable records have been kept since 1972 and especially since 1977 when pelt tagging requirements were implemented. The following table presents a summary of the Montana lynx harvest since 1972. Figure 1. presents the Montana lynx harvest (via mail survey) from 1950 through 1977, when pelt

YEAR	# LYNX	LYNX PELT PRICE
1972-73	300	$ 20.25
1973-74	260	45.00
1974-75	163	80.96
1975-76	250	200.00
1976-77	39	146.00
1977-78	23	210.48
1978-79	58	348.33
1979-80	33	252.25
1980-81	49	290.83
1981-82	53	202.00

1982-83	59	211.25
1983-84	69	260.61
1984-85	36	398.95
1985-86	20	477.14
1986-87	12	475.00
1987-88	10	360.00
1988-89	8	244.00
1989-90	9	145.00

It has been suggested that these harvest data may be suspect or at least confounded for several reasons. Fur dealers point out that prior to the 1977 pelt tagging requirements, bobcat pelts may have been improperly identified as lynx. The pelt tagging requirement and the accompanying harvest restrictions may reflect a significantly reduced harvest aside from any population decline. Lynx from neighboring states and/or provinces may have been included in the Montana data.

THE PROBLEM

It is generally agreed and acknowledged that present Montana lynx numbers are at or near the lowest levels in the past several decades. Despite significant limitations, the harvest data clearly indicate a declining population with only slight evidence of an expected population expansion during the 1980's. A limited number of lynx track winter survey routes in the better lynx areas of region one show that lynx are essentially absent. Winter track counts in

small mountain ranges between the Blackfoot and Clarkfork
rivers show a fraction of the numbers that were present
during 1980-1984.Trappers and field biologists are reporting
a general lack of lynx indications during recent seasons.
Two trappers have reported seeing a few tracks only. Hare
numbers appear to have fluctuated somewhat during the 1980's
with some notable increases during the past few seasons;
however, no recognizable increase in lynx numbers has been
apparent. In fact, lynx numbers appear to continue to
decline, Idaho and Washington have also noted stable or
declining small populations at best.

THE RESPONSE

Lynx season closure in Region one was advocated by Tom
Hay as long as 5 or 6 years ago and by Region 3 personnel
about 3 years ago. Region one formally recommended the
entire closure of the lynx harvest season for the 1989-90
season with the support of many local trappers and Montana
trappers Association members and officers. The season was
not closed because Region 2 and 3 did not also recommend it
and falling pelt prices and increasing hare numbers were
thought to favor lynx increases somewhat. Region one will
again recommend a lynx closure for the 1990 - 91 season. A
meeting of MTA members in Region 2 resulted in a motion to
close the lynx season. The motion died for lack of a
second.

Low lynx numbers and long term population welfare are
a concern of the Montana Chapter of the National Wildlife

Federation. The Federation has called for the closure of the lynx season and a trapping closure above 5000 feet elevation for all large animals. Fish, Wildlife and Parks has corresponded with the Federation.

OTHER JURISDICTIONS

Washington and Idaho have small viable lynx populations They have not closed their lynx seasons; however, both states have a very limited number of permits; 3 and 2 respectively. They apparently believe these very conservative harvest quotas will protect their limited populations. Most Canadian Provinces are placing some protective quotas on lynx harvest during low population segments of the lynx cycle. Alberta has closed some of its southern regions during low population levels. They concluded from the most comprehensive lynx research effort to date that it is simply not sound management to continue to trap a lynx population with essentially zero recruitment for the 3 to 5 year combined period during the most severe portion of the decline and the initial stages of recovery. Alaska has curtailed harvests on the Keni Penensula and other areas subject to overharvest.

OPTIONS AND CONSIDERATIONS

There is some legitimate question as to whether an absolute lynx closure would in fact produce less actual lynx mortality than a very low quota system. Man-caused lynx mortality is not going to cease entirely if the season is closed. There will be incidental captures associated with

bobcat and coyote trapping in lynx habitats. These may go largely unreported during a closed season and carcass information will be lost. Some illegal trapping of lynx will continue under either system. Some trappers have expressed concern that once the season is closed , it will probably never be reopened, and that they would support a closure only if specific provisions to reopen the season once the population recovery has occurred, are written into the closure. It may be true that we (DFWP) may never have enough information to justify another harvest season. It is probably reasonable to conclude that a very low quota system and a closed season would provide very similar overall protection to lynx. Spokespeople from the fur trade are forcasting the further decline of lynx pelt values and they believe that low prices will provide all the relief from harvest pressure that is needed. Some trappers point out that a closed season has never been needed before and ask "Why Now?"

The Federation urges the Department to take the most conservative option and close the season until sufficient data exists to justify reopening it. They further state that " It may well be that lynx seasons are unwarranted in Montana except during years when populations are at levels reached during the mid 70's." They further believe that maintaining an open season with insufficient data is not only potentially destructive to the resource, but further polarizes public attitudes regarding consumptive use of

wildlife. They urge the Department to close the lynx season and use other methods available to benefit lynx before lynx management becomes a controversial and contentious issue involving groups who are opposed to trapping under all circumstances.

MANAGEMENT PROGRAM

An improved lynx management program should be placed into effect starting with the 1990 -91 season, regardless of which harvest scheme is adopted. The minimum information required to manage lynx for a population recovery or a sustained harvest of surplus animals from healthy populations or to reopen a harvest season following a period of closure should include the following:

1. Collection of reliable lynx harvest data on pelt tagging forms.

2. Implementation of an adequate winter lynx track survey through habitat known to contain lynx during good population levels.

3. The collection of snowshoe hare density and trend information in sufficient amounts to enable an accurate assessment of the hare population status.

4. Collection of carcasses to evaluate fecundity, sex and age structure.

5. Annual evaluation of results from lynx and hare surveys, lab work and pelt price information and formulate harvest quotas based on these data.

RESEARCH NEEDS

The life history, basic biology and the ecology of the lynx is well understood and adequate documentation exists. However, there is an almost total lack of information on the quantative and qualatative details of the lynx-hare cycle and the associated levels of energetics. Little or no information exists on the prey density required to trigger various levels of fecundity. Information on the effects of trapping during various stages of the hare cycle is generally lacking. There is a total absence of information regarding the possible relationship between Canadian and Montana lynx populations as well as the general dynamics of a peripheral population in much different habitats such as Montana. Unlimited research opportunities exist with the lynx; however, comprehensive research on this species will be extremely expensive and long term.

The puma is a fresh meat eater and a big-game hunter that seems to prefer deer to any other prey. It captures, among other wild mammals, the porcupine, cottontail rabbits, and varying hare in considerable numbers, and occasionally other rodents and small carnivores. At times it will kill an elk. It seldom molests birds. Of the domestic stock, it seems to prefer horses, especially colts, and, next in order, cattle, though it also will attack sheep and pigs. Of the puma in Clark County woods in 1878 it was written, "it has already killed a cow and two yearling calves" (*Clinton Independent*, September 18, 1878). In making its kill, the puma does not run its prey and attack from below as does the wolf, but captures it by lying in wait or stealthily creeping upon it and then making a quick rush and springing on the back or side of the prey. It often consumes the entire animal, but any remains are usually covered with soil, leaves, or debris; the puma may return after two or three days for further feeding. Sometimes the prey which is left may be consumed by other carnivores.

In Wisconsin the puma had no natural enemies other than man. External parasites believed to infest the species in North America include the louse *Trichodectes felis*; the ticks *Dermacentor variabilis, Ixodes ricinus*, and *I. cookei*; and the flea *Arctopsylla setosa*. Internal parasites include the nematode *Physaloptera praeputialis* and the cestodes *Echinococcus granulosus, Taenia taeniaformis*, and *T. lyncis*. Rabies is the only disease known to affect the puma seriously.

The puma has little economic value except as an object for hunting and trapping sport, and as an aid in reducing excess deer populations when hunting does not control the surplus. Its pelt has little value except as a trophy. We might like to have a few in the wilderness areas of Wisconsin and may regret its passing from our fauna, but its presence in any numbers in a dairying country could not be tolerated. When its natural food of deer, rabbits, and porcupines is scarce, farmers have heavy losses from its depredations on domestic stock.

Specimens examined from Wisconsin.—Only 1, as follows: *Outagamie County:* Appleton (near), 1 (type specimen, UWZ, No. 13,464).

Selected references.—Anonymous, 1947 b; Jackson, H.H.T., 1955; Schorger, A. W., 1938; Scott, W. E., 1939 b; True, F. W., 1891; Young, S. P., and E. A. Goldman, 1946.

Genus Lynx Kerr
Lynxes and Bobcats

Dental formula:

$$I\frac{3-3}{3-3}, \quad C\frac{1-1}{1-1}, \quad P\frac{2-2}{2-2}, \quad M\frac{1-1}{1-1} = 28.$$

Lynx canadensis canadensis Kerr
Canada Lynx

Lynx canadensis Kerr, Animal Kingdom, vol. 1: systematic catalogue between pp. 32 and 33, and p. 157, 1792.

Lyncus borealis Lapham, p. 43, 1852; Lapham, p. 339, 1853.

Lynx Canadensis Strong, p. 436, 1883.

Lynx canadensis Snyder, p. 126, 1902; Jackson, p. 25, 1908; Hollister, p. 26, 1910; Cory, p. 287, 1912.

Lynx canadensis canadensis Komarek, p. 205, 1932; Barger, p. 11, 1952.

Vernacular names.—Usually called lynx in Wisconsin, and in colonial days often called *loup cervier* (French Canadian). Other names include *be-jew* or *pe-zu* (Chippewa), catamount, gray wildcat, *le chat* (French Canadian), *loupcervier*, lynx cat, and *pichu* (French Canadian).

Identification marks.—A rather large cat, about twice the weight of a big domestic cat, with comparatively short and robust body; prominent tufts of hair on the ears and ruffs on the cheeks and below the jaws; very short furry tail with black tip all around; long limbs and especially large broad feet; eyes prominent; nose short and broad; fur, particularly in winter, long, fine, and silky. In full autumn or winter pelage the general color of the upper parts is pale


Lynx   Bobcat

*Side view profile of heads of Canada lynx and bobcat.*

grizzled buff gray, more or less mixed with buffish
or pale brown, the top of the head more brown-
ish; inside of ears grayish white, the tips of the
ear tufts and lines down margin black; cheeks and
nose grayish; ruff on cheeks and throat dark,
a mixture of blackish, gray, and brown; under
parts pale, grayish white or grayish buffy white,
sometimes with a few spots of blackish, especially
on inside of legs; tail pale buffy gray with tip
black all around. The worn pelage late in spring
is more buffy than the winter fur. The fresh sum-
mer pelage is darker and more brownish than
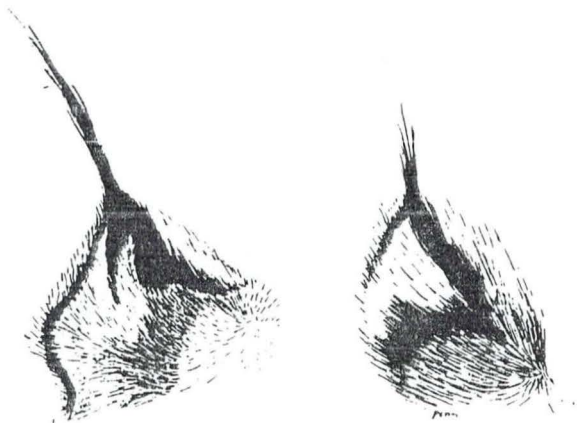
*Ears of Canada lynx and bobcat, drawn from Lake
States specimens.* ⅗×.

Basilar parts of skulls of LYNX RUFUS, *left, and* LYNX
CANADENSIS, *right, to show differences in shape of
presphenoid bones and in placement of anterior
condyloid foramina.* ⅗×.
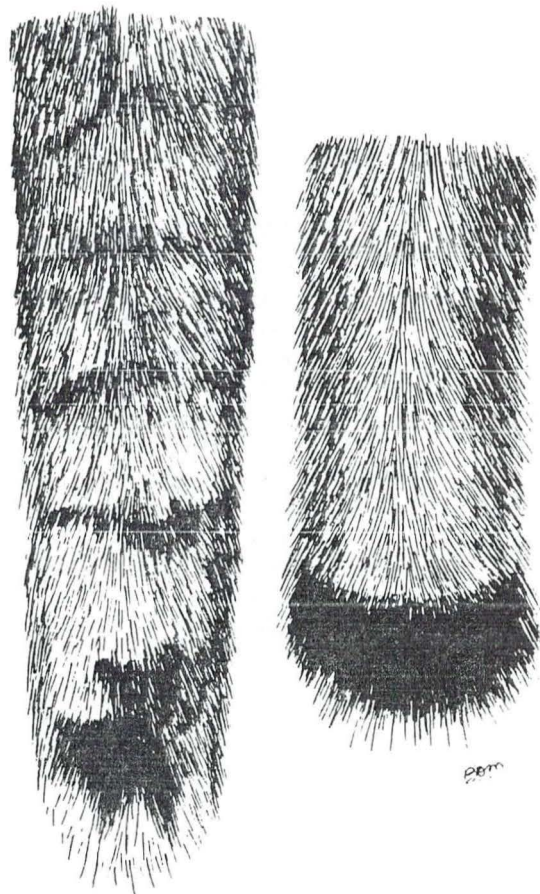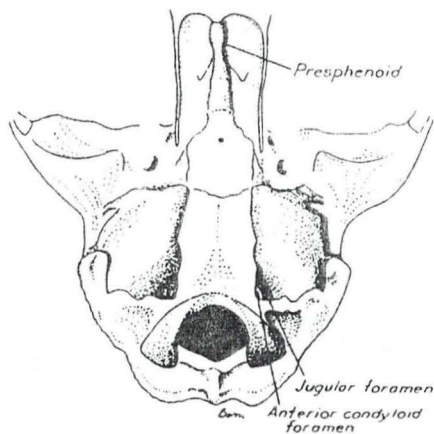
Tails of bobcat, left, and Canada lynx, right. ¾×.

Canada lynx. Photograph by W. J. Banks. Courtesy of W. A. Swallow, editor, Our Dumb Animals.
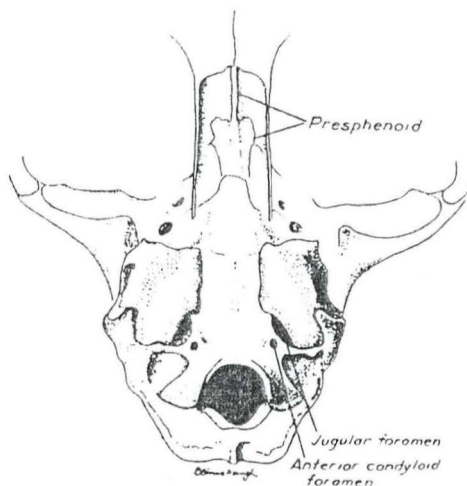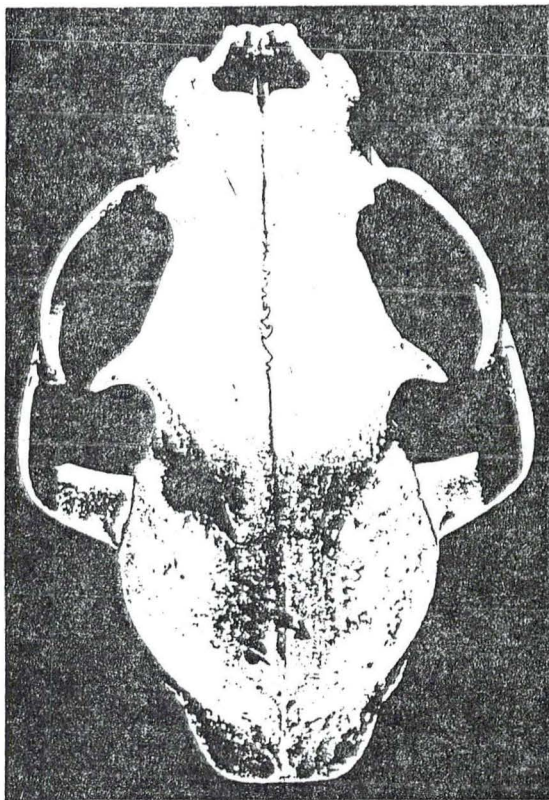
Skull of LYNX C. CANADENSIS, *Oxford House, Manitoba.* ¾×.

Left hind foot of Canada lynx. 1×.

full winter fur. Apparently there is only one molt a year which occurs late in spring. The difference between summer and winter fur and coloration is due to continuous growth of the hair during autumn, the long silky hair with grayish tips being acquired by late in autumn or early in winter. The immature lynx is paler and more buffy than the adult, and is spotted and dashed with darker brown and blackish.

The skull of the lynx is low and broad, much smaller than that of the puma (always less than 160 mm. broad), and has one less upper premolar on each side, a total of 28 teeth as in the bobcat. The skull of the lynx is usually larger than that of the bobcat, though occasionally a
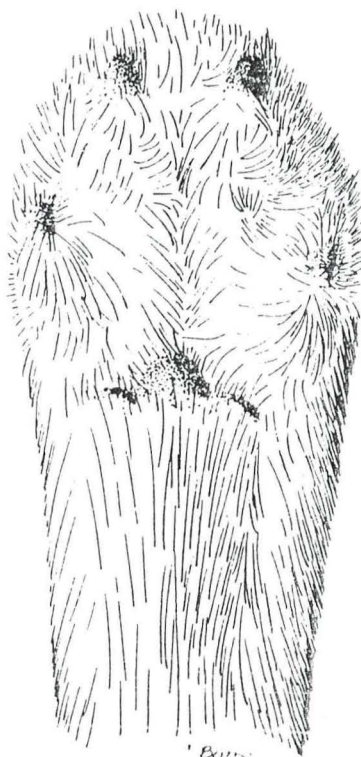
small lynx skull may be smaller than a large bob-cat skull; relatively and actually smaller audital bullae; broader interorbitally, usually more than 30 mm. (always less than 30 mm. in the bob-cat); flatter in facial area (prefrontal and pos-terior maxillo-nasal region) and less compressed laterally; presphenoid wide posteriorly, more than 6 mm. in greatest width; anterior condyloid foramen separate from foramen lacerum poste-rius (comfluent foramina in bobcat); condyle of ramus shorter in extero-interior diameter; denti-tion heavier; length of upper carnassial more than 16 mm.

The male lynx averages slightly larger than the female, possibly about 5 per cent, and in old individuals tends to develop a more pro-nounced saggital ridge. The more or less spotted young drop the spots from the upper parts as the fur develops, and attain adult pelage their first winter. Thereafter no color change associated with age of the animal occurs other than the occasional paling and raggedness of extreme senility. Individual variation is normal, though what may be mutations have been mentioned as "drab-blue" and "fawn or yellow" (Jones, S. V. H., 1923).

The lynx is apt to be confused only with the bobcat, from which it differs in the solid black all around tip of tail, longer ear tufts, and huge feet, twice as long as the tail. Skull characters previously mentioned are also distinctive.

Measurements.—Total length of adult, 875 to 1,000 mm. (34.5 to 39.2 in.); tail, 100 to 120 mm. (3.9 to 4.7 in.); hind foot, 215 to 250 mm. (8.4 to 9.8 in.). Weight of adult, 16 to 35 pounds, occasionally heavier. The specimen UWZ No. 14,607, adult female from Hurley, Iron County, Wisconsin, weighed 8390 grams (18.5 pounds). An adult male from Spring Green, Sauk County, weighed 27 pounds when shot (Schorger, 1947: 186). Skull length, 122 to 146 mm.; width, 92 to 108 mm.

Distribution in Wisconsin.—Formerly probably throughout the entire state in wooded areas, ap-parently more frequently in the northern half of the state, though never common. Now very rare and erratic in distribution.

Habitat.—Heavy and dense forests and wood-lands.

Status and Habits.—The Canada lynx has never been common in Wisconsin, and fur rec-ords early in the nineteenth century indicate that only a few of its pelts were sold each year, though its fur was highly desirable. In 1803-1804, Michel Curot (1911: 410) purchased a few in the region of Yellow Lake and the St. Croix River, Burnett County; in 1804, Victor Malhiot (1910: 221) procured some at Lac du Flambeau, Vilas County; and in 1814 and 1816 lynx pelts were procured near Green Bay (Thwaites, 1910 c: 429). Numerous records of the Canada lynx occurring in various parts of the state were made available in newspapers or reports until about 1880, a few of which may have referred to the bobcat or even the puma, but many of which were authentic. Recognition of the differences in the three species seems to have been surprisingly common. Possibly the extensive lumbering oper-ations and forest disturbances during the last years of the nineteenth century may have been a contributing factor to the near extirpation of the lynx during that period. It will always be a rare mammal in Wisconsin, yet comparatively recent records from widely separated localities such as Middleton, Dane County, 1907, Spring Green, Sauk County, 1946 (Schorger, 1947),
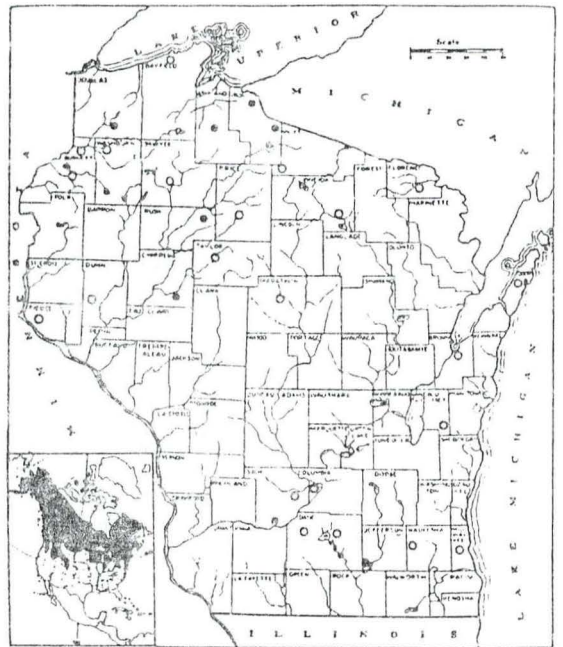
Map 73. *Distribution of* LYNX CANADENSIS. ● = *specimens examined.* ○ = *authentic records.*

Chippewa County, 1908 (Scott, W. E., 1951), and Hurley, Iron County, 1954 (John T. Emlen, Jr., in litt. April 6, 1955) indicate that a few might continue to be with us.

I have accepted as reliable two recent records reported by Doll, Balser, and Wendt (1957):

There have been other unverified reports recently. Dewey Yeager, Conservation Department trapper, and John Waggoner reported jumping and running a lynx on January 22, 1956, in Washburn County; the animal was not captured. This was in T41 and 42N, R12W. Donald Balser, game manager with the Conservation Department at Cornell, reported seeing lynx tracks in the Chequamegon National Forest in Taylor County (about twenty miles southeast of the Rusk County record) during the latter part of November, 1955. It seems probable that a low remnant population has persisted and, with the increased forest cover in northern Wisconsin, may be slowly increasing throughout the area.

In Canada, where the lynx sometimes is not uncommon, it has cycles of abundance. "Hudson's Bay Company and some other records provide a record of lynx (*Lynx canadensis*) fur collections for 206 years. . . . The cycle in lynx furs is very violent and regular and has persisted unchanged for the whole period. Its average period is about 9.6 years" (Elton and Nicholson, 1942: 243). The lynx may wander many miles to new country, and particularly during the winter may travel 50 miles or more over a favored route, yet near its established breeding home it usually confines its range to a radius of less than 5 miles.

A Canada lynx may inhabit a neighborhood for a long time unknown to human dwellers. Any kill of game or small domestic stock left uneaten by a lynx may be suspected to be the discard of some other predator, unless the unmistakable big, round, evenly spaced tracks are evident. Feces, claw marks, scratches, and other signs usually are unidentifiable, especially from those of the wildcat. The lynx, active both summer and winter, is almost strictly nocturnal, though sometimes it is out mornings or during the daytime if hungry. It is not a fast runner, and usually when traveling faster than a walk, runs in a near trot, rarely breaking into a clumsy gallop. It travels well on snow, particularly if slightly crusted, its large feet acting, as it were, like snowshoes. Its fastest running speed probably is not more than 12 miles an
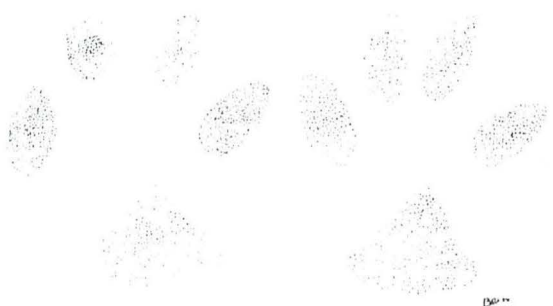
Tracks of Canada lynx. Left, right fore foot. Right, right hind foot. ½×.

hour, though it has never been accurately determined. It jumps exceedingly well, and from a standing posture or a slow walk can leap 15 or more feet. It takes to water voluntarily and swims well, with its head and shoulders well out of water.

The lynx is a solitary animal that rarely assembles in a group, and then of only three or four animals, probably a mother and young. It has most of the vocal attributes of a house cat—purrs lightly, hisses through bared teeth and with upturned nose in defense, growls when distressed or disturbed, mews to its kittens, and, especially during the mating season, utters a terrific yowl or cry. In writing of one that came to Durward's Glen, Caledonia Township, Sauk County, previous to 1880, Dorward (1901: 116) tells us that it "tarried quite a while within easy gunshot, screaming in a blood-curdling manner all the time," and that it "was too dark to see it, but the scream was considered sufficient identification." The lynx has a rather sullen disposition. It is extremely inquisitive, and frequently will follow a person in the wilderness for many miles, with no intent to attack. David Cartwright, referring to the Gilbert Creek region, Dunn County, in December, 1858, writes: "We found that a lynx had followed my track for several miles after I had left the deer the night before" (Cartwright and Bailey, 1875: 243). Muscular and agile, the lynx nevertheless tires easily and frequently rests crouched in a convenient location. Its endurance, however, against cold, famine, and injury are phenomenal. Its senses are well developed, especially that of sight, hence the expression "lynx-eyed" and the north Eurasian

legend that the European lynx had the ability to see through thick stone walls. Its potential longevity possibly is near 15 to 18 years. The longevity record for the National Zoological Park is 11 years and 4 months (Mann, 1930: 303).

Mating takes place in January or February, and after a gestation period of about 62 days the one to four—rarely five—young are born in March or April. The only description we have of a newly born lynx is that published by C. Hart Merriam:

"It was dropped" writes Mr. [Montague] Chamberlain, "on the 20th March, 1883, when the mother had been in captivity about a month. She gave birth to five (5) kittens, but this was the only one rescued from her unmotherly jaws. When the first was born she at once prepared to clean it, and seemed fond of it. After a short time, however, it gave vent to a weak squeal, which caused her to eye it curiously for a moment, when another squeal was delivered. This settled the kitten's doom—it was at once devoured. The mother did not exhibit any tenderness towards the other four, and the keeper made two unsuccessful efforts before he was able to get one away from her. The kitten lived two days, and then died from injuries received in its removal from the cage. Its 'mew' was something like that of a domestic kitten, but stronger and harsher; it was almost fierce and very penetrating. The general strength of the animal was greater than that of a domestic kitten. Two hours after birth it stood firmly on its feet and turned around in its box, but it did not show any inclination to fight when teased. The eyes were open at birth." (Merriam: 1886:10).

More recent observations indicate that normally the young are born with closed eyes that open in about nine or ten days. The kitten is much more brownish than the adult and is streaked and blotched on the upper parts and blotched and spotted on the flanks and under parts, the markings gradually disappearing until adult pelage is acquired at about nine months of age. There is only one litter a year, and the young one becomes sexually mature at the end of its first year. The mammae are four, two abdominal and two inguinal.

The den where the young are reared is in a hollow tree, stump, or log, and sometimes under fallen timber. The nest consists of leaves, bark, and similar vegetative matter pawed and trampled into form by the parent. Similar dens are sometimes occupied as shelters, but as a rule the

lynx prefers to rest crouching on top of a rock, log, or knoll where it has vantage to attack its prey or escape a possible enemy.

Rabbits, particularly snowshoe rabbits, are the chief prey of the lynx, normally constituting probably 90 per cent of its food. It also captures grouse and squirrels, and is a natural enemy of the red fox, which it kills and consumes. Rarely, it eats porcupine, but is sometimes killed by the quills when it does. It seldom consumes deer, and its wilderness habitat gives it little contact with domestic stock. Prey usually is consumed where killed, and any remains are left uncovered. The predator may return to the quarry for other meals as long as the flesh is not putrid, but it prefers fresh meat. The lynx is one of our most strictly carnivorous mammals and never eats vegetable matter except rarely to chew a little grass. There are records of its attacking its own kind, and a case of cannibalism occurred in northern Ontario in March, 1951, when a large lynx attacked and killed one of two young lynxes that were hunting snowshoe rabbits, and ate the flesh from the hind legs and as far forward as the kidneys (Elsey, 1954). It attacks its prey by patiently lying crouched in waiting and giving a tremendous leap onto its victim, and never follows its prey for more than two or three jumps.

Enemies of the lynx other than man are negligible. Probably many kinds of parasites infect it, as with most carnivores, among which are the external parasites *Ceratophyllus dentatus*, *C. labiatus*, and *C. petriolatus*, *Foxella ignotus*, and *Hoplopsyllus glacialis*, and the internal parasites *Taenia laticollis* and *T. rileyi*.

The lynx is a potential fur producer. Its pelt brings $20 to $25 on the fur market, and sometimes, as in 1922, choice pelts bring as high as $80 each. It is so rare now in Wisconsin as to have little economic importance, and the few trapped are taken along with wildcats for bounty payment. It is not a regular domestic stock killer, and no forester would oppose its disposing of snowshoe rabbits that are so harmful to forest nursery stock. It is comparatively easy to trap. Any protection given the lynx would favor the wildcat.

Specimens examined from Wisconsin.—Total 11, as follows: *Ashland County:* Cayuga, 3 (UWZ). *Chippewa County:* Sec. 27, T 28 N, R 6 E, 1

Population and habitat characteristics of lynx and snowshoe hares in north central Washington

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Lynx (*Lynx canadensis*) and snowshoe hare (*Lepus americanus*) population characteristics and use of habitats were studied during 1985–1987 in north central Washington. Lynx used areas above 1463 m elevation that were dominated by lodgepole pine (*Pinus contorta*) and Engelmann spruce – subalpine fir (*Picea engelmannii – Abies lasiocarpa*) cover types. Snowshoe hares were the most common prey of lynx, with remains of snowshoe hare occurring in 23 of 29 scats. Counts of tracks and pellets showed snowshoe hares to be most abundant in 20-year-old lodgepole pine stands. Fire suppression and natural fire frequencies in the past 5 decades has limited the amount of these early successional forests, which are important as habitat for snowshoe hares. Marginal habitat conditions for snowshoe hares probably resulted in a scarcity of prey in the study area and may explain the relatively large home ranges of lynx (69 ± 28 km^2 for five males and 39 ± 2 km^2 for two females), low density of adults (2.3 lynx/100 km^2), and high kitten mortality rates (88% for eight kittens in three litters). Demographic characteristics of lynx in the study area may be representative of lynx populations along the southern periphery of their range where habitat conditions are marginal for lynx and snowshoe hares.

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Les populations de Lynx (*Lynx canadensis*) et de Lièvres d'Amérique (*Lepus americanus*) ont fait l'objet d'une étude en 1985–1987 dans le centre-nord du Washington, afin de déterminer leurs caractéristiques démographiques et leur répartition dans l'habitat. Les lynx utilisaient les zones les plus élevées, au-dessus de 1463 m d'altitude, dominées par les couvertures de Pins vrillés (*Pinus contorta*) et de complexes Épinettes d'Engelmann – Sapins subalpins (*Picea engelmannii – Abies lasiocarpa*). Les lièvres constituaient les principales proies des lynx et ont été retrouvés dans 79% de 29 fèces examinées. Le dénombrement des pistes et des excréments a révélé que les lièvres abondaient particulièrement dans les forêts de Pins vrillés de 20 ans. Les mesures adoptées pour enrayer les feux de forêts et la fréquence peu élevée des feux naturels au cours des cinq dernières décennies a réduit le nombre de forêts en début de succession, si importantes pour les lièvres. Les conditions marginales disponibles aux lièvres ont probablement causé une rareté de proies dans la région d'étude et peuvent expliquer les dimensions relativement importantes du domaine vital des lynx (69 ± 28 km^2 chez cinq mâles et 39 ± 2 km^2 chez deux femelles), la faible densité des adultes (2,3 lynx/100 km^2) et le taux élevé de mortalité des petits (88% chez huit petits en trois portées). Les caractéristiques démographiques des lynx dans la région étudiée représentent probablement celles des populations de lynx le long de la frontière sud de leur domaine où les conditions sont marginales à la fois pour les lynx et pour les lièvres.

[Traduit par la revue]

Introduction

Lynx (*Lynx canadensis*) are found over most of Alaska and Canada, and their presence in Washington, Idaho, Montana, Utah, Colorado, and Wyoming marks the southern limits of their range in western North America (McCord and Cardoza 1982). Studies in Alaska and Canada have provided an understanding of lynx population dynamics and prey requirements at northern latitudes (Saunders 1963*a*, 1963*b*; van Zyll de Jong 1966; Nellis and Keith 1968; Nellis et al. 1972; Brand et al. 1976; More 1976; Brand and Keith 1979; Parker et al. 1983; Ward and Krebs 1985; Bailey et al. 1986), but little is known about lynx at southern latitudes.

At northern latitudes, lynx numbers fluctuate approximately every decade in response to fluctuations of snowshoe hares (*Lepus americanus*), their principal prey (Elton and Nicholson 1942; Keith and Windberg 1978). For these areas Brand and Keith (1979), Parker et al. (1983), and Bailey et al. (1986) recommended restricting lynx harvest during periods when numbers and productivity were low.

At southern latitudes, lynx populations dynamics may differ from northern latitudes because snowshoe hare numbers do not radically fluctuate (Chitty 1950; Dolbeer and Clark 1975; Wolff 1980). Because these peripheral populations may be highly vulnerable to overharvesting and habitat disruption, an under-standing of the dynamics of populations at southern latitudes is needed to manage lynx responsibly.

Reported here are the results from a study of an unexploited population of lynx and snowshoe hares in north central Washington. The study was carried out during 1985–1987 by the Wildlife Research Institute and the Idaho Cooperative Fish and Wildlife Research Unit in cooperation with the Washington Department of Wildlife. These study findings are compared with radiotelemetry studies conducted at the same site by the Washington State Department of Wildlife during 1980–1983 (D. Brittell, unpublished data).

Site description

The study area (1795 km^2) was located in Okanogan County, north central Washington, and borders Canada (latitude 49°N, longitude 120°W). Elevations within the study area ranged from 750 to 2540 m. Temperatures ranged from −23 to 35°C and mean annual precipitation was 51 cm at 660 m elevation (National Oceanic and Atmospheric Administration). During winter, i.e., November–April, snow depths exceeded 1 m above 1980 m elevation.

Major forest associations included Douglas-fir (*Pseudotsuga menziesii*) and ponderosa pine (*Pinus ponderosa*) at elevations below 1370 m and on southerly aspects at higher elevations.

Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) were the dominant associations at higher elevations, with lodgepole pine (*Pinus contorta*) and aspen (*Populus tremuloides*) the dominant seral tree species (Williams and Lillybridge 1983).

Carnivores inhabiting the area include lynx, mountain lions (*Felis concolor*), bobcats (*Lynx rufus*), coyotes (*Canis latrans*), black bears (*Ursus americanus*), and martens (*Martes americana*). Potential prey of lynx in the area include snowshoe hares, red squirrels (*Tamiasciurus hudsonicus*), ground squirrels (*Spermophilus columbianus*), deer mice (*Peromyscus maniculatus*), and voles (*Microtus* spp. and *Clethrionomys* sp.).

Methods

Lynx were captured in box-type live traps and padded No. 3 leg-hold traps during winter and summer. Animals were anesthetized with 20 mg ketamine hydrochloride/kg estimated body weight. They were weighed, measured, and classified as adults or kittens based on weight, size, and association with adult females. Lynx were individually marked with an identifying eartag, tattoed in the ear and lip, and fitted with a radio-transmitting collar.

Lynx use of space and forest cover types and lynx reproduction and mortality were determined for radiocollared animals. Lynx movements were monitored by telemetry from an airplane at 7- to 15-day intervals and from the ground at 1- to 7-day intervals. Accuracy of telemetry locations was approximately 12 ha and was determined by locating transmitters placed in the field. Elevation and universal transverse mercator (UTM) grid coordinates were recorded for each location from United States Geological Survey 15-min topographic maps.

The minimum convex polygon method (Hayne 1949) was used to estimate size of home-range areas to compare results with studies of lynx conducted elsewhere. Because the number of locations influences convex polygon home-range size estimates (Jennrich and Turner 1969), the number of locations plotted against home-range sizes (Odum and Kuenzler 1955) indicated >20 observations were required to provide reliable estimates of individual home ranges. Therefore annual home-range sizes were calculated for individuals with ≥22 locations annually from 1 April to 31 March (period of breeding to dispersal of kittens).

Density of lynx was estimated in a 648-km² centrally located portion of the study area using radiotelemetry, snowtracking, and capture–recapture techniques. Snowtracking and radiotelemetry surveys were conducted daily along roads transecting the area. The roads from which surveys were conducted were <5.6 km from the 1463- and 2133-m contours, the elevational range where radiocollared lynx were located. Since 5.6 km was less than or equal to the width of home ranges for all radio-collared animals, it was assumed that uncollared lynx would have either crossed the road or the tracks would be encountered during periodic surveys into areas not occupied by radio-collared animals. These methods provided a relatively thorough survey of 570 km² of available habitat, based on geographical information system (GIS) inventories (see below). Unmarked and marked lynx were identified from concurrent snowtracking and locations of radio-collared animals or captures. Lynx tracks occurring in areas not occupied by radio-collared lynx were assumed to be made by unmarked animals. The total number of lynx in the 648-km² area includes radio-collared and unmarked animals. Although density estimates may underestimate the number of transients present, movements of radio-collared lynx during this and the previous study (D. Brittell, unpublished date) indicates that there were few transients in the area.

Movements of radio-collared females were monitored daily during spring and early summer to determine whether or not females were denning. Restricted movements and (or) daily returns of females to a location suggested that individuals might be denning, and sites were inspected to record the number of kittens. The numbers of kittens accompanying females during October–November were determined from snowtracking to calculate kitten survival rates during summer.

Annual survival rates for radio-collared adults were estimated from daily survival rates (Trent and Rongstad 1974).

A GIS computer digitizer was used to determine the proportion of forest cover types occurring within a home-range area. These values were compared with the proportion of forest cover types occurring within the 1795-km² study area to determine if forest cover types in areas occupied by lynx differed from that available above 750 m elevation. Forest cover type maps were constructed for the study area using the United States Forest Service LANDSAT imagery based GIS, which was designed to inventory forest cover types and forest fuels. Five forest cover types were identified: (*i*) stands with >25% canopy cover of ponderosa pine and open grassland – sage brush (*Artemisia* spp.), which occur primarily on xeric sites on south aspects and at elevations below 1370 m; (*ii*) Douglas-fir, western larch (*Larix occidentalis*), and aspen stands that occur on more mesic sites at elevations near 1370 m and on south aspects at higher elevations; (*iii*) forests with >40% canopy cover of Engelmann spruce and subalpine fir and occurring on mesic sites mostly above 1370 m; (*iv*) stands with >40% canopy cover of lodgepole pine; and (*v*) alpine sites with open meadows and rocky peaks and occurring above 2000 m elevation. These five categories were selected to minimize discrepancies that may occur between cover types identified by LANDSAT and those identified from on-site inspection and aerial photography. The selection of these types also minimized misclassification because of interspersion of cover types and decreased the numbers of types to minimize the likelihood of a type II error in χ^2 goodness of fit tests (Alldredge and Ratti 1986; White and Garrot 1986).

Den sites were investigated again in late summer, after females abandoned sites, to record UTM coordinates, elevation, aspect, forest association (Williams and Lillybridge 1983), age of dominant and subdominant tree species, and number of logs intercepting a 50-m transect line contouring the slope from den sites.

Lynx scats were collected and the contents compared with a reference collection to determine animal species eaten. The frequency of occurrence of items in scats was assumed to be equivalent to their importance in the diet. During winter, lynx were snowtracked to determine hunting strategies and successes.

Snowshoe hare use of forest cover types was determined from counts of fecal pellets along 67 transect lines. Transect lines (each 100 m long) were spaced at ≥325-m intervals perpendicular to the road that bisected the study area. This spacing was selected to ensure independence of counts between transect lines and assumed that home-range sizes of snowshoe hares were <8.8 ha (Wolff 1980). Transect lines were placed in the forest cover types occupied by lynx. These were subdivided into age-class categories and include (*i*) lodgepole pine stands <20 years old; (*ii*) lodgepole pine stands 43 years old; (*iii*) lodgepole pine stands >82 years old; (*iv*) mature (>100 year old) Engelmann spruce – subalpine fir stands; (*v*) Douglas-fir, western larch, and aspen stands, and (*vi*) meadows. A minimum of five transects were placed in each of these six forest types, with the number of transects in each type being proportional to the estimated area of each type within the study area. Ten circular plots of 1 m radius were positioned at 10-m intervals along each 100-m transect. After plots were cleared of pellets in September 1986, pellets were counted and removed from each plot in June 1987, after snowmelt, and in September 1987 to determine habitat use in winter and summer, respectively.

During winter, the number of snowshoe hare tracks were counted along 65 transects 100 m in length. These transects, located along the road, were positioned within 50 m on both sides of the intercept to the pellet plot transects. Tracks were counted from 24 to 36 h after a snowfall, with each transect surveyed eight times during the winter. Intensively used ""runways"" were counted as 3, 6, 9, or 12 tracks, depending on use.

Elevation, aspect, habitat association (Williams and Lillybridge 1983), stand age (by increment boring), dominant and subdominant overstory tree species, and shrubs were recorded for snowshoe hare sample plots. Stand density was determined by counting the number of tree and shrub stems in four size classes (<2.5, 2.5–10.0, 10.1–37, and

:⁻ cm diameter at breast height (dbh)) within a 25-m² plot at the ...,dpoint of each transect line. The species and dbh of trees and shrubs browsed by snowshoe hares in the study area were tallied to determine their relative use as food during the winter.

Statistical tests

The number of snowshoe hare pellets on each transect was summed for each winter and summer season and was normalized using a square-root transformation (Zar 1984). Differences in winter and summer pellet counts among cover types were analyzed using analysis of variance and Tukey's method of multiple comparisons (Zar 1984). Track counts from the eight surveys were summed for each transect. Kruskal–Wallis tests and Tukey-type multiple comparisons (Zar 1984) were used to examine differences during winter of snowshoe hare track counts among cover types and differences of stand densities among cover types. Spearman's rank order correlation (Zar 1984) was used to measure the relationship between winter pellet counts and winter snowshoe hare track counts and relationships between snowshoe hare pellet and track counts among stand densities. Wilcoxon rank sum tests were used to compare seasonal use of elevation by lynx.

Results

Lynx home-range size and density

From 1985 to 1987, five adult male and two adult female lynx were captured and their movements monitored by telemetry for 346–765 days each. In addition, two kittens <6 weeks old were captured and eartagged but not radiocollared. Mean home-range size, based on 22–48 locations, was 39 ± 2 (SD) km² for the two females and 69 ± 28 km² for the five males (Table 1). Lynx used the same home ranges during all seasons and for more than 2 years. Male ranges overlapped female ranges completely.

Based on 362 radiotelemetry locations, 31 captures and sightings, and >5600 km of winter travel during track and radiotelemetry surveys by snowmobile and skis, 15 adults were known to occupy the 640-km² core area (2.3 adults/100 km²). During the winter of 1985–1986, no kittens were identified in the study area, but during 1986–1987 snowtracking indicated that four kittens were present. The mean annual density of adults and kittens over the 2-year period was 2.6 lynx/100 km².

Productivity and survival

In July 1986, two radio-collared females had litters with three and four kittens each. These two females had litters again in July 1987; one female had only one kitten and the other female had at least one kitten, but the litter size was not determined. Monitoring the radio-collared females following inspection of den sites for kittens indicated females did not abandon den sites; therefore, it is assumed that my activities did not contribute to kitten mortalities. Snowtracking in the winter of 1986–1987 and the winter of 1987–1988 indicated that only one of the eight kittens (12%) from the three litters of known size survived to winter. In addition to these litters, snowtracking indicated that an uncollared female was accompanied by three kittens during the winter of 1986–1987. Therefore, four kittens survived to the winter of 1986–1987, and no kittens survived to the winter of 1985–1986. Snowtracking indicated that kittens accompanied females until March or April when 9–10 months old. Annual survival rates of radio-collared adults were 0.73 for 1986 and 1.00 for 1987. One adult male apparently died from predation and one died from unknown causes.

Lynx use of elevations and forest cover types

Lynx were located at higher elevations ($P < 0.05$) during summer ($x = 1787$, range 1463–2133 m) than during winter ($x = 1738$, range 1536–2024 m). Radio-collared lynx used lodge-

TABLE 1. Home-range sizes (minimum convex polygon) of lynx in north central Washington, 1985–1987

Animal No.	Total days monitored	Home-range size (km²)	
		1985–1986	1986–1987
Females			
111–167	765	38 (43)	38 (48)
112–71	594	41 (22)	
Males			
55–87	346		56 (27)
104–90	460		88 (39)
109–62	719	99 (26)	
59–11	384	74 (33)	
195–58	607	29 (33)	

NOTE: The number of locations per home-range size estimate is in parentheses.

TABLE 2. Percentage (mean and range) of forest cover types indentified by GIS within home-range areas of radio-collared lynx ($n = 7$) and within the 1795-km² study area above 750 m elevation in north central Washington, 1985–1987

	Home ranges		
Forest cover type	Mean (%)	Range (%)	Study area (%)
Lowland grassland – ponderosa pine	1.7	0.3–3.0	15.2
Douglas-fir – western larch – aspen	12.8	7.8–17.2	27.5
Englemann spruce – subalpine fir	25.0	15.8–33.8	20.6
Lodgepole pine	57.3	46.7–65.8	31.8
Alpine	3.2	1.3–5.9	5.0

pole pine and Engelmann spruce – subalpine fir forest cover types in greater proportion than expected and used xeric lowland forest types less than expected ($\chi^2 = 42.1$, df = 4, $P < 0.001$; Table 2). Snowtracking showed that lynx crossed open meadows ≤100 m in width but did not hunt in these areas. During winter, lynx crossed silviculturally thinned areas >100 m in width that had no understory cover nor shrubs and had 420–640 trees/ha.

Four denning sites were characterized as mature (≥250 years old) stands with an overstory of Engelmann spruce, subalpine fir, and lodgepole pine. All denning sites were located on north–northeast aspects, with an average of 40 downfall logs/50 m. Kittens were observed using the down logs for escape cover.

Prey of lynx

Remains of snowshoe hare were found in 23 and remains of red squirrels in 7 of the 29 lynx scats examined. Remains of fawn deer, adult deer, and white-footed deer mice each were found in a single scat. Remains of snowshoe hares and red squirrels were also found at den sites. Snowtracking lynx for 20.5 km indicated that they chased snowshoe hares on six occasions and squirrels on two occasions and captured two snowshoe hares and no squirrels during those attempts.

Snowshoe hare use of forest cover types

Winter snowshoe hare pellet counts differed among cover types ($F = 20.49$, df = 5, $P = 0.0001$) with the highest counts ($P < 0.05$) in 20-year-old lodgepole pine stands (Table 3). Pellet counts during summer 1987 were also different among the four cover types sampled ($F = 10.56$, df = 3, $P = 0.0003$). Twenty-year-old lodgepole pine stands also had the highest

TABLE 3. Mean number of snowshoe hare tracks ($\pm$SD) and mean number of snowshoe
hare pellets ($\pm$SD) during winter (spring 1987 count) and summer (fall 1987 count)

Dominant overstory	Age (years)	Mean no. of tracks/100 m	Mean no. of pellets/m^2	
			Winter	Summer
LP	20	$10.9\pm7.2a$ (5)	$25.4\pm14.8a$ (5)	$3.7\pm3.5a$ (5)
LP	43	$8.9\pm3.1a$ (9)	$4.9\pm2.1b$ (11)	$1.3\pm0.9ab$ (5)
LP	>82	$5.8\pm3.9ab$ (18)	$6.4\pm7.1b$ (18)	—
SSAF	>100	$2.8\pm1.9b$ (15)	$2.7\pm2.2bc$ (15)	$0.7\pm0.9bc$ (6)
DFWLA	>43	$2.3\pm2.6b$ (13)	$0.9\pm0.9cd$ (13)	$0.03\pm0.05c$ (7)
Meadow		$1.4\pm2.5b$ (5)	$0.0d$ (5)	—

NOTE: Counts followed by the same letter were not significantly different ($P > 0.05$, Tukey multiple comparisons tests). The number of transects sampled is in parentheses. LP, lodgepole pine; SSAF, Engelmann spruce and subalpine fir; DFWLA, Douglas-fir, western larch, and aspen.

TABLE 4. Spearman's rank-order correlations between stand density and snowshoe hare use measurements

Stem diam. (cm)	Winter pellets		Fall pellets		Winter tracks	
	r	P	r	P	r	P
<2.5	0.62	0.0023	0.55	0.0082	0.53	0.0155
2.5–10	ns		ns		ns	
10–37	ns		ns		ns	
>37	ns		ns		ns	
Total	0.64	0.0013	0.56	0.0068	0.80	0.0001

TABLE 5. Dominant overstory species, age, and density of trees and shrubs (measured in 25-m^2 plots along transects) within five forest cover types sampled for snowshoe hares

Dominant overstory	Age (years)	Mean no. of stems/ha	Mean no. of stems <2.5 cm dbh/ha
LP	20	16 320	15 840
LP	43	4 800	1 360
LP	82–200*	—	—
SSAF	100–200	2 960	1 360
DFWLA	43–200	720	80
Meadow	—	0	0

NOTE: Species abbreviations as in Table 3.
*Stems not tallied.

pellet counts in summer, but differences in pellet counts between the 20- and 43-year-old lodgepole pine stands were not significant (possibly owing to small sample sizes).

Snowshoe hare track counts showed a habitat-use pattern similar to that of pellet counts, with lodgepole pine stands having more hare tracks than Engelmann spruce – subalpine fir, Douglas-fir – western larch – aspen, and meadow cover types ($F = 12.28$, $df = 5$, $P = 0.0001$; Table 3). Winter pellet counts and winter snowshoe hare track counts were significantly correlated ($r = 0.71$, $P < 0.001$), suggesting these two indices provide similar information on the use of habitats by snowshoe hares.

Snowshoe hare track and pellet counts were correlated with density of tree and shrub stems <2.5 cm in diameter and the total numbers of trees and shrubs (Table 4). Twenty-year-old lodgepole pine stands had the highest total number of stems ($\chi^2 = 9.26$, $df = 3$, $P = 0.026$) and stems <2.5 cm in diameter ($\chi^2 = 9.6$, $df = 3$, $P = 0.022$; Table 5). Also, lodgepole pine

trees <2.5 cm in diameter make up 96% of tree stems browsed ($n = 372$) by snowshoe hares. All lodgepole pines browsed that were >2.5 cm in diameter ($n = 8$) were bent to the ground by snow, and only the tips of the trees were browsed. Snowshoe hares ate the bark on stems and often consumed whole stems <10 mm in diameter.

Discussion

Habitat use of lynx and snowshoe hares

Snowshoe hares are the primary prey of lynx in the study area, as well as throughout its range (Saunders 1963b; van Zyll de Jong 1966; Nellis and Keith 1968; Nellis et al. 1972; Brand et al. 1976; More 1976). Lynx use of lodgepole pine forests, where snowshoe hares were most abundant, is consistent with other studies showing that lynx use habitats where snowshoe hares are most abundant (Parker 1980; Koehler et al. 1979; Bailey et al. 1986). Based on pellet counts, the density of snowshoe hares was four to five times greater in the 20-year-old stands than the older (43 or ≥82-year-old) stands of lodgepole pine and nine times greater than Engelmann spruce – subalpine fir stands. These 20-year-old stands, where average density of trees and shrubs <2.5 cm dbh was 15 840 stems/ha, likely provided the forage and escape and thermal cover required by snowshoe hares (Wolff 1980; Pietz and Tester 1983; Litvaitis et al. 1985). Densely stocked stands are characteristic of snowshoe hare habitat (Adams 1959; Wolfe et al. 1982; Litvaitis et al. 1985; Fuller and Heisey 1986). In Alaska, snowshoe hares preferred habitats where the density of trees and shrubs was 22 027 stems/ha (Wolff 1980), and in Maine hares were most abundant in stands with > 16 000 softwood stems/ha (stems ≤7.5 cm dbh and >0.5 m tall, Litvaitis et al. 1985).

Besides thermal and security cover, the 20-year-old lodgepole pine stands offered the greatest amount of browse for hares during winter. Although lodgepole pine seedlings and alder (*Alnus sinuata*) occurred within the 20-year-old stand, lodgepole pine was the primary browse for hares during winter (96% of stems browsed), and alder was used little (<1%). *Salix* sp., *Acer* sp., *Populus* sp., *Betula* sp., preferred browse for hares elsewhere (Klein 1977; Conroy et al. 1979; Wolff 1980; Fox and Bryant 1984), were uncommon in the study area.

Lodgepole pine forests ≤20 years old made up <10% of the study area above 1460 m elevation where lynx occurred, whereas mature Engelmann spruce / subalpine fir and lodgepole pine forests ≥43 years old were present over >80% of the area. Although 20-year-old lodgepole pine stands had the highest snowshoe hare densities in the study area (25.4 pellets/m^2), the densities were lower than in habitats where hares were most

...dant in Alaska (81.5 pellets/m², Bailey et al. 1986) and ...ova Scotia (65 pellets/m², Parker 1980).

Influences of prey abundance on lynx home-range size, density, reproduction, and mortality

The scarcity of prey may explain the large home ranges, low density, low productivity, and high kitten mortality of lynx during this study. During this study, minimum convex polygon home-range sizes of 38–99 km² were larger than reported for radio-collared lynx in Alaska (13–26 km², Berrie 1973) and Nova Scotia (8–33 km², Parker et al. 1983) but compare in size with lynx home ranges in Minnesota (51–243 km², Mech 1980), Montana (43–122 km², Brainerd 1985), Manitoba (138 and 177 km², Carbyn and Patriquin 1983), and Alaska (50–783 km², Stephenson 1985, Bailey et al. 1986).

Although the number of radiotelemetry locations used in calculations may influence the size of home-range estimates, Mech (1980) suggested that low prey abundance may have contributed to the large-sized home ranges of lynx colonizing Minnesota. Ward and Krebs (1985) documented a threefold increase in the home-range sizes (13–39 km²) for lynx in the Yukon when snowshoe hare numbers decreased from 14.7 to about 0.2 hares/ha. The predominance of mature habitats in the study area suggests that prey populations were low, and lynx may have required large-sized home ranges to obtain enough food to sustain themselves.

Densities of 2.1 lynx/100 km² (D. Brittell, unpublished data) during 1980–1983 and 2.3 lynx/100 km² during 1985–1987 were similar to the 2.3 lynx/100 km² reported in Alberta when snowshoe hare numbers were low (Brand et al. 1976) and 1–2.3 lynx/100 km² in Alaska where lynx were heavily harvested (Bailey et al. 1986). When snowshoe hare numbers were at a high in the population cycle, lynx densities approached 20 animals/100 km² in Alaska (Bailey et al. 1986) and Nova Scotia (Parker et al. 1982) and 8–10 animals/100 km² in Alberta (Brand et al. 1976). During 1976–1981, 14 lynx were harvested from the study area, suggesting harvest may have contributed to the low density, but factors other than harvesting maintained the low density on the study during 1982–1987 when harvest was curtailed.

Productivity was low during the study, with zero to four kittens present during the winters 1985–1987, and zero to two kittens present during the winters 1980–1983 (D. Brittell, unpublished data). The low number of kittens produced is comparable to lynx populations at northern latitudes when snowshoe hares were scarce. In Alaska, the percentage of kittens in the harvest decreased from 40 to 2% (Berrie 1973; O'Conner 1986) as the number of snowshoe hares declined, while the percentage decreased from 29 to 2% in Nova Scotia (Parker et al. 1983). The mean age of 4.5 years for 14 lynx harvested in the study area during 1976–1981 (D. Brittell, unpublished data) compares with a mean age of 3.6 years for lynx in Alberta when snowshoe hare numbers declined and 1.6 years when hares were plentiful (Brand and Keith 1979) and suggests that reproduction on the study area was low prior to 1981. During periods of snowshoe hare scarcity, when consumption rates are about 20% below the normal maintenance level for wild lynx (Brand et al. 1976), lynx productivity declines (Brand and Keith 1979; Parker et al. 1983; O'Conner 1986).

The high mortality of kittens, too, suggests that prey may have been scarce. Although kitten survival was not determined in the study area during 1980–1983 when eight females were monitored (D. Brittell, unpublished data), the number of kittens in the population each winter was similar during these two studies, 1981–1983 and 1985–1987. The kitten mortality rate of 88% documented for this study was similar to mortality rates of 65–95% in Alberta during a 3-year period when prey populations were declining (Brand and Keith 1979) and females likely were unable to obtain enough food (Brand et al. 1976; Brand and Keith 1979). During periods of increasing snowshoe hare numbers, kitten mortality may be only 20% (Brand and Keith 1979). The preponderance of mature forests and scarcity of prey may explain the low survival rate for kittens during this study and may be why denning females foraged 6–7 km from den sites.

A scarcity of snowshoe hares may not result in a substantial use of red squirrels. Although squirrels were common in the study area (Koehler et al. 1990) and occurred in 24% of the lynx diet, more energy may be required to capture squirrels (capture rate of tree squirrels was estimated as half that for snowshoe hares (Nellis and Keith 1968), and energy gains from a diet of squirrels are less than those from snowshoe hares (five to seven squirrels were equivalent to one hare (Nellis and Keith 1968; Brand et al. 1976)). Therefore, a diet of squirrels may not be adequate to ensure lynx reproduction and survival of kittens.

The 7-year period (1980–1987) of low kitten production in the study area was similar to the 5-year period of low productivity at northern latitudes when prey was scarce (Brand et al. 1976), possibly indicating that snowshoe hare populations were at a cyclic low during the study period and that they may soon rebound. However, snowshoe hare numbers may not cycle at southern latitudes as they do further north; instead, densities may be lower and remain relatively stable over time (Chitty 1950; Dolbeer and Clark 1975; Wolff 1980; Sievert and Keith 1985). At southern latitudes, because of the greater heterogeneity of habitats and smaller amounts of optimal habitat (Windberg and Keith 1978; Wolff 1980; Sievert and Keith 1985), hares are more vulnerable to increased mortality from predation (Dolbeer and Clark 1975; Windberg and Keith 1978; Wolff 1980; Sievert and Keith 1985) that would limit the density of hares and in turn limit the density of lynx (Windberg and Keith 1978; Brand and Keith 1979). Similar correlations between latitude and cyclic and noncyclic populations have been documented for voles and their predators, stoats (*Mustela erminia*) and owls (*Aegolius funereus*), in Fennoscandia and Scandinavia (Erlinge et al. 1983; Hansson and Henttonen 1985; Linden 1988; Korpimaki and Norrdahl 1989).

Fire suppression in the past 5 decades has limited the young-aged early successional forests in the study area, as well as in the entire region, as it has in some areas of the Great Lake States (Fox 1978). Early successional forests beneficial to snowshoe hares in the study area resulted from lightning fires and windthrow. These existed as small, isolated islands within the study area and rarely exceeded 1 ha in size, smaller than the hare home-range sizes of 8.8–10 ha (Adams 1959; Wolff 1980). Although snowshoe hare populations may show localized fluctuations within areas of optimal habitat (Fox and Bryant 1984), suboptimal habitats may not provide for increases in snowshoe hare numbers in the study area. This and the heterogeneity of habitats may explain Chitty's (1950) observations that snowshoe hare numbers may not fluctuate in southern British Columbia.

If snowshoe hare numbers do not fluctuate but remain relatively stable over time, reproductive rates of lynx may remain low and relatively stable over time. This may explain the few kittens present in the study area during 1980–1987 and the older ages for harvested lynx during 1976–1981.

Although productivity may be low in the study area,

recruitment may benefit from periodic immigration from British Columbia. Lynx emigrate from Ontario into Minnesota as lynx numbers increase in Canada each decade (Mech 1980).

Prey scarcity and the low productivity of lynx, as shown in this population, may be characteristic of peripheral populations where habitat is marginal. Habitat conditions and prey scarcity may limit the southern distribution of lynx by affecting productivity.

Managing lynx populations and their habitats at southern latitudes

Although it has been shown that harvest may have little negative impact on numbers of lynx when prey is abundant and production of kittens is high (Quinn and Thompson 1987), harvest may negatively affect lynx populations during periods of prey scarcity when kitten survival is low (Brand and Keith 1979; Carbyn and Patriquin 1983; Parker et al. 1983; Bailey et al. 1986). During times of prey scarcity, recruitment is low and may not compensate for losses created by harvest mortalities (Brand and Keith 1979). Compared with canids, felids show a reduced capacity to respond quickly when their populations decline as a result of fluctuations in prey base or exploitation pressure (Eisenberg 1986).

The vulnerability of lynx to trapping and the influences of trapping on lynx survival rates is shown by the high mortality rates (50–90%) in areas where lynx were harvested (Mech 1980; Carbyn and Patriquin 1983; Parker et al. 1983; Ward and Krebs 1985; Bailey et al. 1986) compared with the low mortality rate (0–27%) in the study area where lynx were protected. In addition, trapping females accompanied by kittens would result in orphaned kittens possibly dying from starvation (Carbyn and Patriquin 1983). During periods of prey scarcity, lynx populations may become increasingly vulnerable to exploitation as they abandon home-range areas in search of prey (Ward and Krebs 1985). This has also been demonstrated for marten (Thompson and Colgan 1987).

Ward and Krebs (1985) and Bailey et al. (1986) pointed out the need for large refugia for maintaining lynx populations during periods of low recruitment. Lynx in the 2944-km^2 Riding Mountain National Park in Manitoba were vulnerable to trappers outside the park, and Carbyn and Patriquin (1983) concluded that the park was not large enough to sustain a viable population of lynx.

There are no large unexploited population centers of lynx that could act as a reservoir from which animals might immigrate into the study area. Only 350 km^2 of potential habitat (based on GIS inventories of lodgepole pine, Englemann spruce, and subalpine fir forests) occurs in protected adjacent areas, supporting fewer lynx than were found in the study area where there was 570 km^2 of habitat. British Columbia likely provides the largest contiguous area of habitat for lynx adjacent to the study area, but timber harvesting and trapping there may limit immigration of lynx into the study area.

Controlled harvest levels should be limited to years of high population recruitment (Brand and Keith 1979; Parker et al. 1983; Bailey et al. 1986). This is crucial where habitat is limited and immigration from unexploited populations is minimal (Parker et al. 1983). In marginal habitats, as in the study area, lynx may be highly vulnerable to overexploitation, and extreme caution must be exercised when considering harvest regulations. For these areas, close population monitoring would be necessary.

High trophic level carnivores require closer monitoring than more abundant herbivore populations (Gluesing et al. 1986).

Monitoring would require field surveys to be conducted, since harvest data alone would not be adequate. As demonstrated for lynx (Ward and Krebs 1985) and marten (Thompson and Colgan 1987), changes in trapper success may not accurately reflect changes in population levels, as animals disperse from home range areas and become increasingly vulnerable to trapping when prey becomes scarce.

Monitoring population trends would require winter tracking surveys to be conducted. Areas should be surveyed more than three times each winter to minimize variability because of snow conditions, lighting conditions, and the experience of personnel conducting the survey.

GIS inventories of potential habitats for lynx are needed to provide regional estimates of lynx numbers for population management and to identify areas for habitat management. Management of forest pests, timber harvesting, and road access are needed to minimize these impacts. Natural or prescribed fires and timber harvesting will have negative short-term impacts because of reduced security cover for lynx and snowshoe hares, but the successional forests would benefit hares and lynx (Brocke 1975; Fox 1978; Conroy et al. 1979; Parker et al. 1983; Monthey 1986) and can be managed to enhance habitat conditions for lynx. However, forest management would require that (*i*) the number and size of openings be limited, (*ii*) early successional forests as habitat for prey be encouraged, and (*iii*) mature forest be protected for denning habitats.

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Snowshoe Hare, *Lepus americanus*, Use of Forest Successional Stages and Population Changes During 1985-1989 in North-central Washington

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Snowshoe Hare (*Lepus americanus*) pellet counts along 24 permanent transects in north-central Washington showed hare numbers to be greatest in ≤ 25-year-old successional forests. Observations of numbers of hare tracks during winters indicated that hare numbers did not peak or crash during 1985-1989. Compared to more northern latitudes where numbers of hares change 6-100-fold during 2-5 year intervals, pellet counts showed hare numbers on the study area decreased 1.5-fold from 1986 to 1989. Observations that hare numbers either do not fluctuate or the cyclic changes in hare numbers are greatly dampened within the study area supports the hypothesis that Snowshoe Hare populations do not radically fluctuate at southern latitudes.

Key Words: Snowshoe Hares, *Lepus americanus*, population cycles, successional forest stages, Washington.

While Snowshoe Hare (*Lepus americanus*) numbers are known to cycle every 8-11 years at northern latitudes (Elton and Nicholson 1942; Keith and Windberg 1978; Keith 1981), they do not show such radical fluctuations at the southern periphery of their range (Chitty 1950; Dolbeer and Clark 1975; Wolff 1980, 1981; Keith 1981). Understanding the habitat requirements and dynamics of regional Snowshoe Hare populations has important ecological and management implications. To assess Snowshoe Hare use of forest successional stages and possible changes in hare numbers in north-central Washington I compared counts of Snowshoe Hare fecal pellets among four successional forest stages between September 1986 and September 1989 and compared observations of relative numbers of hare tracks present each winter from 1985 through 1989.

Study Areas and Methods

The study area was located in north-central Washington (48° 50'N, 119° 52'W) between elevation 1536-1952 m (Koehler 1990). Wild fires and timber harvesting have produced a mosaic of successional forest stages, including mature forests where Engelmann Spruce (*Picea engelmannii*) and Subalpine Fir (*Abies lasiocarpa*) predominate and younger-aged forest where Lodgepole Pine (*Pinus contorta*) is the dominant overstory tree. Because numbers of Snowshoe Hare fecal pellets are reliable estimators of Snowshoe Hare numbers (Litvaitis et al. 1985a; Krebs et al. 1986), I compared counts of pellets among successional forest stages and between years 1986 and 1989 to determine use of habitats and to assess changes in numbers over time. Fecal pellets were counted along 24 permanent transects within the four most prevalent successional forest states (six transects successional stage). Based on species and average age (determined from increment boring) of dominant overstory trees the four successional stages included: (1) forests with a Lodgepole Pine overstory ≤ 25 years old, (2) Lodgepole Pine forests ~ 46 years old, (3) Lodgepole Pine forests > 80 years old, and (4) Engelmann Spruce Subalpine Fir forests > 100 years old. Transects were 100 m long and spaced at ≥ 325 m intervals along and perpendicular to the road that bisected the study area. This spacing was selected to ensure independence of counts between transects and assumed that home range sizes for hares were < 8.8 ha (Wolff 1980). Ten 1-m radius circular plots were positioned at 10 m intervals along each 100-m transect. Pellets within each circular plot were counted before leaf fall during September 1986 and September 1989. Pellets were counted on the same plots during both years and it was assumed that pellet decomposition rates were similar for both periods. Pellets were summed for each transect and the mean number of pellets among the four successional stages were compared within years using ANOVA and Tukey's method of multiple comparisons (Zar 1984). Counts between 1986 and 1989 were compared using paired t-tests. I also made observations of Snowshoe Hare tracks each winter from 1985-1989 to determine whether hares were rare, common, or abundant.

Results and Discussion

Pellet counts indicated that Snowshoe Hare numbers were up to 16.0-times more abundant in the ≤ 25-year-old Lodgepole Pine forests than in the older-aged successional stages during 1986

Table 1. Mean number of Snowshoe Hare pellets/m² within successional forest stages in north-central Washington during 1986 and 1989 (n = 6 transects, successional stage). Counts followed by a common letter were not significantly different (P > 0.05, Tukey multiple comparisons tests).

Successional	1986	1989
Forest Stage	Mean ± SD	Mean ± SD
Lodgepole Pine ≤ 25 yrs	15.8 ± 13.3A	14.9 ± 6.1 A
Lodgepole Pine ~ 46 yrs	12.7 ± 7.1 A B	5.2 ± 2.5 B
Lodgepole Pine > 80 yrs	5.9 ± 5.1 A B	2.8 ± 1.8 B
Engelmann Spruce/Subalpine Fir > 100 yrs	1.0 ± 0.7 B	1.4 ± 1.7 B

(F = 4.3, P = 0.02) and 1989 (F = 18.1, P < 0.001). Koehler (1990) observed Snowshoe Hares to be more abundant in these ≤ 25-year-old Lodgepole Pine forests where density of tree and shrub stems averaged 16 320 stems/ha than in the older-aged successional forests where stem density averaged ≤ 4800 stems/ha. Densely stocked stands are important for the forage, escape, and thermal cover they offer Snowshoe Hares (Adams 1959; Wolff 1980; Wolfe et al. 1982; Pietz and Tester 1983; Litvaitis et al. 1985b; Fuller and Heisey 1986).

Average counts of Snowshoe Hare pellets in 1986 [x ± SD = 8.9 ± 9.5 pellets/m²] were 1.5 times greater than in 1989 (6.0 ± 6.3 pellets/m², differences between years were significant t = 2.2, P = 0.04), suggesting that Snowshoe Hare numbers declined during this period. However, comparisons of pellet counts within each successional stage between years (Table 1) indicated only counts in the approximately 46-year-old Lodgepole Pine forests were significantly different (t = 3.0, P = 0.03). Differences between years within ≤ 25-year-old Lodgepole Pine, > 80-year-old Lodgepole Pine, and Engelmann Spruce/Subalpine Fir successional stages were not significant (P > 0.05). The 1.5-fold decrease in pellet counts within the study area and 2.5-fold decrease within ~ 46-year-old Lodgepole Pine successional stage during three years compares to a 6-100-fold change in Snowshoe Hare numbers during 2-5 year intervals at more northern latitudes (Brand and Keith 1979; Parker et al. 1983; Ward and Krebs 1985).

The slight (1.5-fold) change documented from pellet counts during this study and observations of Snowshoe Hare tracks each winter indicating no peak or crash in hare numbers from 1985-1989 suggests that Snowshoe Hare populations in the north-central Washington study area remained relatively stable. Although caution is required when extrapolating these findings to longer time periods or to larger areas (Wiens et al. 1986) these data indicate that although annual variations in

numbers of hares may occur, the typical "cycle" may either be lacking or dramatically dampened within the study area. Surveys conducted during the 1930-1940s indicate Snowshoe Hare numbers may not show the regional fluctuations in the western United States (Chitty and Elton 1937) or in southern British Columbia (Chitty 1950). Similar correlations between latitude and population dynamics have been documented in Fennoscandia and Scandinavia for small rodents (Hansson and Henttonen 1985; Linden 1988). The relatively stable Snowshoe Hare populations at southern latitudes may, in part, result from a lack of large sized areas of optimal habitat (Chitty and Elton 1937; Dolbeer and Clark 1975; Keith 1981; Wolff 1981). Indeed, the young-aged Lodgepole Pine successional stages where Snowshoe Hare numbers were most abundant existed as small isolated pockets, fragmented by a diversity of exposure, slopes, soils, elevations, and older-aged forest cover types. Fire suppression in the past five decades has affected the patterns of forest succession in the study area too, reducing the amount of optimal habitats for hares and undoubtedly affecting the dynamics of hare populations.

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Managing Spruce-Fir Habitat for Lynx and Snowshoe Hares

Lynx are commonly found (shaded area) among the boreal forests of Alaska and Canada and the spruce, subalpine fir, and lodgepole pine forests in the mountains of the West.

Long winters, deep snow, thin soils, and fires have helped shape the Engelmann spruce *(Picea engelmannii)*, subalpine fir *(Abies lasiocarpa)*, and lodgepole pine *(Pinus contorta)* forests in the mountains of the western United States.

Until recently, development of remote high-elevation forests has been discouraged by the high cost of timber harvesting, processing, and reforestation. Markets for firewood, fuel pellets, house logs, posts, and pulpwood are placing new demands on these forests and their wildlife. Legislative mandates and public concern require that wildlife values be considered along with management of other forest resources.

Lynx *(Lynx canadensis)*, commonly associated with the boreal forests of Alaska and Canada, are also found among the isolated spruce, subalpine fir, and lodgepole pine forests in the mountains of the West. Lynx, the only members of the cat family in North America adapted to the cold winters and deep snows of northern latitudes, occur above 4,000 feet in Washington, Idaho, and Montana, above 6,500 feet in Wyoming, and above 8,000 feet in Colorado and Utah. The low numbers and dispersed populations within the West make lynx vulnerable to overexploitation and habitat disruption. However, understanding their habitat and prey requirements and incorporating this into forest planning will help ensure a better position for lynx within some western forests.

We gathered information on lynx

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habitat and prey requirements during radio telemetry studies of lynx from 1980 to 1987 in north-central Washington (Koehler 1990). This information, together with findings from studies elsewhere, is presented as a guide to be integrated with forest and wildlife management objectives for high-elevation forests in the West. Where management for lynx is a concern, we offer suggestions for monitoring the population responses of lynx to habitat alterations.

A Specialized Predator

Lynx are similar in appearance and size (15–25 pounds) to the bobcat *(Lynx rufus)*. However, lynx have longer tufts of fur on the tips of their ears, their tails are tipped with black rather than black-barred on the dorsal side, their legs are longer, and their feet are twice the size of those of the bobcat. The large feet and long legs permit lynx to move easily over the snow, enabling them to find a niche at high elevations where snow persists for much of the year.

Unlike other carnivores whose diets may be quite varied, lynx prey almost exclusively on snowshoe hares, *Lepus americanus* (More 1976, Koehler 1990). This dependence on hares as a primary food source has a major influence on the dynamics of lynx populations. In areas where or during periods when hares are abundant, lynx reproduction is high and densities are high; when or where hares are scarce, lynx productivity and densities are low (Brand and Keith 1979, Parker et al. 1983, Koehler 1990).

Conditions favoring snowshoe hares will benefit lynx. But lynx require a mosaic of forest conditions—early successional forests for hunting and

By Gary M. Koehler and J. David Brittell

Providing habitat for lynx is compatible with other forest uses.

mature forests for denning. Although fires, epidemics of forest disease, and logging may have negative short-term effects on lynx by eliminating cover for snowshoe hares and lynx, they may have long-term benefits as succession progresses and snowshoe hares become abundant.

Managing for Prey

Lynx prefer habitats where snowshoe hares are abundant (Saunders 1963, Koehler et al. 1979, Parker et al. 1983). During summer, when cover is plentiful and succulent forbs, grasses, and small shrubs are abundant, snowshoe hares have little difficulty surviving. But during winter, when snow covers low-growing plants, conditions become critical for hares and they must feed on shrubs and seedlings exposed above the snow surface. Small-diameter twigs and new growth (less than 0.4 inch in diameter) are preferred browse during winter, but larger diameter stems may be eaten when conditions become harsh and food is limited (Wolff 1980). Although willows and birches are the normal food of

snowshoe hares in most areas during winter (Klein 1977, Wolff 1980, Litvaitis et al. 1985), conifers may be an important browse in other regions (Adams 1959, Conroy et al. 1979, Peitz and Tester 1983). In Washington, where young hardwoods are not readily available, hares feed almost exclusively on the tips of lodgepole pine seedlings (less than 1 inch in diameter) and bark of taller lodgepole pine trees (Koehler 1990). For browse, softwood and hardwood saplings and seedlings must be taller than the snow depth, yet short enough to be reached. Where snow depths reach 3–4 feet, trees must be 6–8 feet tall (Wolfe et al. 1982) and less than 0.4 inch in diameter (Wolff 1980, Koehler 1990).

Besides browse, hares need habitat that offer protection from predators and extreme cold. In fact, hares may select habitat where security and thermal cover is abundant even if browse is limited (Monthey 1986). Dense stands with 4,690 to 13,440 stems/acre provide for these needs (Brocke 1975, Wolff 1980, Litvaitis et al. 1985, Monthey 1986, Koehler 1990). Extremely dense stands (greater than 40,000 stems/acre) may be of little use to snowshoes if understory cover and browse is sparse (Adams 1959, Litvaitis et al. 1985). Likewise, stands with 1,052–2,954 stems/acre lack adequate thermal and security cover and would be of little use to hares (Brocke 1975, Koehler 1990). Conifer trees are essential as

they offer more security and thermal cover than do hardwoods. Trees 11.5 feet tall would provide the needed thermal and security cover (Brocke 1975).

Habitat for snowshoe hares should be well dispersed among the areas to be managed for lynx. Forest managers must consider that hares may not recolonize clearcuts until 6–7 years after cutting, and that it may take 20–25 years for hare densities to reach their highest levels (Litvaitis et al. 1985), depending on site conditions and type of treatment. As stands become older (greater than 20–30 years old) and stem density declines, security cover and forage production diminishes (Brocke 1975, Koehler 1990).

Since home range areas of snowshoe hares are 20–25 acres (Adams 1959, Dolbeer and Clark 1975, Wolff 1980),

Burned and clearcut areas can provide favorable conditions for snowshoe hares and lynx once seedlings and saplings are established.

units designated to provide habitat for hares should be 20–25 acres or larger. Dense stands of conifers should be interspersed with small areas of hardwoods and conifers for browse (Brocke 1975, Litvaitis et al. 1985). Logging and thinning units less than 40 acres in size encourage natural regeneration of the forest while offering hares forage and cover. During reforestation, it is important to maintain naturally occurring palatable trees and shrubs.

Managing for Denning

Although lynx need early successional forests for hunting, they need mature forests for denning. In Washington, denning sites were typified as lodgepole pine, spruce, and subalpine forests older then 200 years, with north and northeast aspects, mesic habitat associations, and a high density of down-fall logs (greater that 40 logs/150 feet lying 1–4 feet above ground, Koehler 1990). Downed logs and

Lynx use both ends of the forest successional spectrum; young-aged stands where they hunt for snowshoe hares, and mature stands where they have their kittens
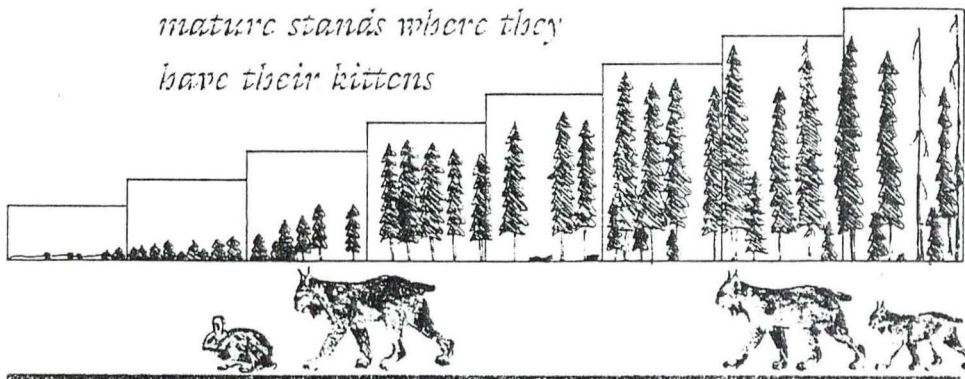
Illustration by Karla Fromm

stumps provide cover for kittens and may be the most important component of denning habitat. Similar habitats are used for denning in Alaska and northern Canada. Although stands used as den sites may range from 1 to 5 acres in size, dispersed pockets of mature stands connected by travel corridors are needed to allow females to move their kittens toward more abundant prey or to avoid disturbances.

Since mature forests support few snowshoe hares (Bailey et al. 1986,

Koehler 1990), it is important that denning areas for lynx be close to prey habitat. One- to five-acre parcels may be adequate as den sites, but these pockets of mature forests must be connected by corridors of cover.

Managing for Cover

Like most wild felids, lynx require cover for security and for stalking prey. This need for cover is shown by their avoidance of large open areas. Typically, lynx do not cross openings wider than 300 feet; however, they do travel through silviculturally thinned stands with 180 trees/acre void of shrubs (Koehler 1990).

Although large openings are avoided by lynx, burned and clearcut areas can provide favorable conditions for snowshoes and lynx once seedlings and saplings become established. To minimize the effects openings may have as barriers to lynx movement, logging units should not be positioned near large meadows, burned areas, or recent clearcuts. Cover should be maintained along ridges and saddles, favored travel routes for lynx. The density of trees should be greater than 180 stems/acre and tree height should be at least 6 feet, particularly where snow depth is 2–3 feet. Clearcuts should be designed less than 300 feet wide so that lynx will cross them, or be irregular in shape with periodic constrictions less than 300 feet wide.

Fire and Forest Management

It is important to coordinate forest management activities to provide a temporal and spatial array of openings (which will mature to snowshoe hare habitat) and early successional and mature forest stands. With this in mind, forest managers should strive for a mixture of openings (natural and artificial) in stands of harvestable-sized timber while maintaining dispersed stands of mature forest.

Fires can play an important role in maintaining habitat for lynx (Fox 1978, Bailey et al. 1986, Quinn and Thompson 1987). Within wilderness and natural areas, wildfires and prescribed fires can provide the early successional forests lynx require. Small fires are less destructive than large fires and create the forest mosaic beneficial to lynx. As

succession progresses, a variety of fire intensities and fire types will contribute to a temporal and spatial pattern of habitat for prey, with unburned areas becoming denning habitat.

For managed forests, recommendations include maintaining mature or old-growth stands for denning and scheduling clearcuts, stand thinning, and prescribed fires to provide a balance of successional stages on the landscape. Although clearcutting and thinning may reduce cover, they can also open the canopy to encourage understory plants beneficial to snowshoe hares. The effects that these activities have on snowshoe hares and lynx depends on timing and manner of treatment. Thinning and logging residue may require treatment to prevent competition for groundcover, shrubs, and seedlings, although some residue should remain as cover for small rodents, prey for lynx and other carnivores. Thinning stands early to maximize tree growth potential can be compatible with hare and lynx requirements provided stands are thinned before hares recolonize the area. Otherwise, thinning should be considered when stands are older than 30–40 years and are little used by hares. Both early and late thinning strategies may be required when integrating timber management objectives with lynx needs. Thinning schedules and size and position of openings may require modification in order to minimize hare depredation of plantation seedlings.

Managing forest diseases and pests requires ingenuity. Although disease and insects may increase fuel loads with increased risk of large, high-intensity fires, they can provide the deadfall needed for cover in denning habitat. As with fire and timber harvesting, disease and insects may contribute to an open forest canopy, encouraging understory shrubs and seedlings. With this in mind, managers of wilderness and natural areas should allow forest disease and pests to follow a more natural course or use fires to control epidemics. In multiple-use management areas where pesticides and herbicides are used, care must be taken to treat only infected areas in order to minimize large openings.

Lynx are vulnerable to overexploi-

tation from trapping (Todd 1985, Bailey et al. 1986). Roads increase access for hunters and trappers, destroy habitat for prey, and disrupt lynx travel and hunting patterns. To mitigate these effects, roads should be kept to a minimum and main roads should be maintained to primitive standards. Lynx travel along roads with less than 50-foot rights-of-way where cover is present on both sides. Therefore, forbs, grasses, shrubs, and seedling trees growing along the edges of roadways should be maintained as cover for lynx and browse for snowshoe hares. Roads should be closed once timber harvest is complete, and physical barriers should be constructed and regulations enforced so that disturbance is minimized.

Monitoring Lynx Populations

Monitoring the response of lynx and hares to habitat alteration is essential, as it may signal a need for changes in forest management strategy. Pellet or track counts are useful techniques for monitoring snowshoe populations. Monitoring populations of the elusive lynx is more difficult.

Snow tracking can be a cost-effective method for monitoring lynx populations over time, but the reliability of this method depends on the observer's experience at identifying tracks, the effect of snow and lighting conditions on the ability to discern tracks, the speed at which the survey is conducted, and the influence of human activities on lynx movement. Where priorities call for managing habitat for lynx, radiotelemetry studies may be needed initially to establish lynx density estimates in order to relate the track count to lynx populations trends.

To minimize variations between track counts, surveys should be conducted several times each month along established routes and within a specified time after snowfall. Consistency of survey design is important, but it may be necessary to survey additional routes once habitat treatment begins, as these activities may alter lynx travel patterns. If rigorously conducted, number of tracks and estimated number of individuals encountered on each mile of survey line (transect, trail, or road) can provide managers with the

Research biologist Tim Koehler holds anesthetized adult lynx. Note long tufts of fur at the tips of the ears and the large feet.

information needed to detect the response of lynx population to habitat manipulation.

Conclusion

Providing habitat for lynx is compatible with other forest resource uses and can be integrated into a forest management program. Prescribed fires, logging, and timber thinning can create the young-aged forests needed as habitat for the principal prey. However, mature forest stands must also be maintained as habitat for denning. The key to managing forests for lynx is to provide a temporal and spatial mosaic of forest age classes. Managing high-elevation forests in the West for both timber and lynx may result in increased management costs initially, but these could be offset by greater economic and ecological diversity. ■

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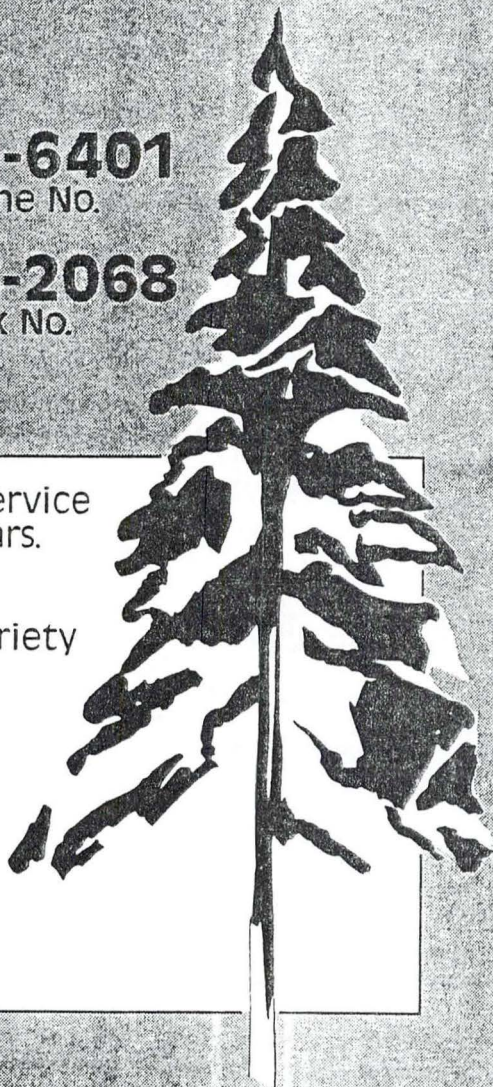WOLFF, J. 1980. The role of habitat patchiness in the population dynamics of snowshoe hares. Ecol. Monogr. 50:111–30.

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Lynx Movements and Habitat Use in Montana[1,2]

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Movements of two Lynx (*Lynx canadensis*) were monitored by radio telemetry: an adult male for 7½ mo from March to October and an adult female during January. Home range area for the male, determined from 21 radio locations, was 36 km². Most locations were in densely stocked stands of Lodgepole Pine (*Pinus contorta*) resulting from the 1910 fires. Snowshoe Hares (*Lepus americanus*), their principle prey, were also most abundant in these stands.

Key Words: habitat, Lynx (*Lynx canadensis*), Snowshoe Hare (*Lepus americanus*), activity patterns.

Little is known about seasonal habitat use or home range size of Lynx (*Lynx canadensis*). Most previous studies used snow-tracking techniques (Saunders 1963; Nellis et al. 1972; Brand et al. 1976). Berrie (1973) used radio telemetry to determine home range size in Alaska. In conjunction with a Wolverine (*Gulo gulo*) study in northwest Montana, we monitored movements of two Lynx seasonally during 1977 by radio telemetry.

Methods

Twenty live-traps were set from January through April along 40 km of Forest Service trail. Traps, measuring 40 × 40 × 65 cm, were constructed of tubular steel frames, chain link fence sides, and sliding steel doors. Lynx were immobilized with ketamine hydrochloride ("Ketalar," Parke Davis) in dosages approximating 21 mg/kg body weight. Lynx were eartagged and tattooed in the lip and on the body under the foreleg, measured, evaluated for general physical condition, and fitted with collars containing radio transmitters. Radio signals were monitored from fixed-wing aircraft and the ground.

The relative abundance of Snowshoe Hares (*Lepus americanus*) in various forest types was obtained by counting the number of tracks crossed per kilometre of trail after fresh snowfall. To help differentiate tracks only those traveling to the west of the trail and spaced 3-m apart were recorded. A vegetative description of each section of trapline included dominant overstory species, age class, and relative density.

TABLE 1—Relative abundance of Snowshoe Hare in four vegetative cover types along trapline during 14 d of survey

| | | | Distance | Tracks | |
Vegetative cover	Stand age, yr	Stand density	surveyed (km)	Total no.	No. km^{-1}·d^{-1}
Lodgepole Pine, pure stands	< 80	Dense	9.0	317	2.54
Grassland islands in dense Lodgepole Pine	< 80	Dense	3.2	96	2.15
Subalpine Fir—Englemann Spruce	Mature > 100	Medium	2.4	15	0.45
Islands of Lodgepole Pine, Douglas Fir, Ponderosa Pine (*Pinus ponderosa*) in grasslands	Mature > 100	Sparse	5.6	11	0.14

Results and Discussion

One adult male (weight 10 kg), one adult female (7 kg), and one juvenile female (4 kg) were captured. The juvenile accompanied the adult female and was not radio-collared because it was too small. The adult female was captured on 14 January and located 8 times prior to being found dead on 31 January. Death was believed due to predation by a Mountain Lion (*Felis concolor*). The male was captured on 10 March and located 21 times by 27 October.

Most locations for the male and female were in young densely stocked stands of Lodgepole Pine (*Pinus contorta*). Twenty-six of the 29 locations (90%) occurred in timbered areas burned in 1910 and the remainder occurred in mature Douglas Fir (*Pseudotsuga menziesii*) – Western Larch (*Larix occidentalis*) stringers along stream bottom within the 1910 burn. Of the locations burned in 1910, 23 (88%) occurred on xeric sites where Lodgepole Pine was dominant and 3 (12%) on mesic sites where Subalpine Fir (*Abies lasiocarpa*) and Englemann Spruce (*Picea englemannii*) were dominant. No locations occurred in open grassland or semi-open areas. 90% were in densely stocked stands, and 10% in medium-stocked stands.

The estimated home range size for the male was 36 km^2. This figure is similar to that found in other studies. Winter tracking in Newfoundland showed a home range size between 15.5 and 20.7 km^2 (Saunders 1963). In Alberta they were from 11.1 to 49.5 km^2 (Brand et al. 1976). In Alaska, Berrie (1973) found Lynx to range from 12.8 to 25.5 km^2.

Snowshoe Hares were most abundant in densely stocked stands of Lodgepole Pine (Table 1). Brand et al. (1976) and Adams (1959) found that hares were most abundant in dense stands. Winter ground tracking during this study and in Alberta (Brand et al. 1976) indicate that Lynx concentrate hunting activity within areas of high hare activity because hares are their main food (Brand et al. 1976) and 90% of Lynx radio locations were in these stands. Saunders (1963) found that Lynx activity and the location of the home range boundary coincided almost exactly with a tract

of 10- to 20-yr-old growth timber.

Our data suggest that Lynx concentrate activity in areas of high Snowshoe Hare activity, particularly in young dense stands of Lodgepole Pine. Radio telemetry indicates that there is no change in range areas or habitat use throughout the seasons.

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The ecology of the lynx (*Lynx canadensis*) on Cape Breton Island

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Recruitment of lynx (*Lynx canadensis*) on Cape Breton Island declined from 1977–1978 through 1979–1980 concurrent with a decrease in snowshoe hare (*Lepus americanus*) densities. Suppressed recruitment resulted from a decline in pregnancy rates, especially in the yearling cohort, and increased mortality of kits during the first 6 months of life. Snowshoe hare was the main component in the diet of lynx during both winter and summer. Lynx rarely travelled together except for females with kits. Hunting success (percent successful chases) increased wth group size. Overall hunting success increased through the winter. Winter kill rates averaged one hare per lynx per 24 h. Home ranges of adults were larger in summer (25–32 km^2) than in winter (12–18 km^2). Daily cruising distances (kilometres per 24 h) were greater in summer ($\sim$9 km) than in winter ($\sim$8 km). Although lynx used all habitats within their home ranges, they selected for the advanced successional habitat ($\sim$20 years after cutting) both winter and summer. Mature conifer habitat was used more in summer than in winter. The short-term impact of extensive forest harvesting within the limited range of lynx on the highlands of Cape Breton Island is uncertain; in the long-term it should prove beneficial by increasing the availability of preferred advanced successional habitat. Harvesting of lynx should be closely controlled, especially during periods of reduced densities of snowshoe hares and suppressed recruitment of lynx.

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Le recrutement du lynx (*Lynx canadensis*) sur l'Ile du Cap Breton a subi un déclin de 1977–1978 à 1979–1980 et il s'est produit en même temps une diminution des densités de population du lièvre (*Lepus americanus*). Ce déclin est le résultat d'une diminution du taux de grossesse, surtout chez les jeunes de l'année, et d'une augmentation du taux de mortalité chez les petits au cours des six premiers mois de leur vie. Le lièvre constituait le principal élément de la diète du lynx, aussi bien au cours de l'hiver que durant l'été. Les lynx ne se déplaçaient que rarement en bandes, à l'exception des femelles et de leurs petits. Le succès de la chasse (pour-cent des poursuites fructueuses) augmentait en fonction de la taille des bandes. Le succès de la chasse a augmenté progressivement durant tout l'hiver. Le taux moyen de capture en hiver était de un lièvre par lynx par 24 h. Les aires vitales des adultes étaient plus grandes en été (25–32 km^2) qu'en hiver (12–18 km^2). Les déplacements quotidiens (kilometres par 24 h) étaient plus importants en été ($\sim$9 km) qu'en hiver ($\sim$8 km). Bien que les lynx aient utilisé tous les habitats disponibles dans leur aire vitale, ils choisissaient de préférence les stades avancés de la succession ($\sim$20 ans depuis la dernière coupe) en hiver et en été. La forêt de conifères à maturité était plus utilisée en été qu'en hiver. L'impact à court terme de la coupe des arbres sur une grande étendue à l'intérieur de l'aire assez limitée du lynx, dans les terres hautes de l'Ile du Cap Breton, est incertain; à long terme, la coupe devrait s'avérer bénéfique en augmentant la disponibilité des habitats en stade avancé de succession. La capture du lynx doit être particulièrement bien surveillée, surtout durant les périodes où la densité des lièvres est faible et où le recrutement des lynx est moins important.

[Traduit par le journal]

Introduction

The Canada lynx (*Lynx canadensis*) is the only wild felid found throughout the boreal forest regions of Canada and Alaska. Owing to its wide distribution and importance to the fur industry, the lynx has received considerable attention, both in the popular and scientific literature.

Newfoundland and Cape Breton Island, Nova Scotia, represent two areas in eastern Canada where lynx are isolated from the continental range of the species. Distribution of lynx on Cape Breton Island is further restricted to the western plateau of Victoria and Inverness counties. That small and isolated population is particularly vulnerable to overharvest. The loss of mature conifer habitat from forest harvesting operations poses an additional threat to the future status of the lynx on the island.

The lynx's cyclical nature in abundance and the close affinity of population fluctuations with changing snowshoe hare (*Lepus americanus*) densities have been well documented (Elton and Nicholson 1942; Wing 1953). Many published reports on lynx describe range extensions (Schantz 1947; Rasmussan 1969), eruptions in numbers (Mech 1973; Gunderson 1978), extensive

individual movements (Nellis and Wetmore 1969; Mech 1977), parasites (van Zyll de Jong 1966*a*), and feeding habits (Saunders 1963*a*; van Zyll de Jong 1966*b*; More 1976).

Studies on the biology and reproduction of lynx have been carried out in western Canada (van Zyll de Jong 1963), Ontario (Stewart 1973), and Alaska (Nava 1970) while general reviews on the status and management of lynx in Canada (de Vos and Matel 1952; Nellis 1971; Van Zyll de Jong 1971) and Alaska (Burris 1971) are also available. Studies on the ecology of natural populations have been conducted in northern Alberta (Nellis and Keith 1968; Nellis et al. 1972; Nellis 1975; Brand et al. 1976; Brand and Keith 1979), Minnesota (Mech 1980), Newfoundland (Saunders 1963*b*), and Alaska (Berrie 1974). This voluminous literature has been skillfully reviewed and analysed by Brand and Keith (1979) to explain demographic changes in lynx during changing snowshoe hare densities.

This paper presents the results of a 3-year study designed to obtain biological and ecological information on the lynx of Cape Breton Island. There had been no earlier studies of lynx in the Maritimes, and results from this study should be interpreted relative to information on lynx from other regions to better understand and manage this discrete population.

Study area and methods

Cape Breton Island forms the northern extension of the province of Nova Scotia, separated from the mainland by the narrow Strait of Canso. A causeway, completed in 1955, joins the two land masses by highway and rail. Physiographically, much of the northwestern portion of the island forms a plateau with elevations reaching 360–390 m. The forests on Cape Breton Island fall within the Acadian Forest Region, while the plateau is subdivided into the Cape Breton Plateau Forest Section (Rowe 1972). Vegetation on the plateau is boreal; the dominant tree species are balsam fir (*Abies balsamea*), white spruce (*Picea glauca*), black spruce (*Picea mariana*), and white birch (*Betula papyrifera*). Peat bogs and heath-shrub barrens are scattered throughout.

The study area was on the southeast portion of the highlands (Fig. 1) and included habitat types common throughout the Cape Breton Plateau. The area was cover-typed from aerial photographs and described from summer ground checks. The original study area during 1977–1978 contained 58.5 km^2 and included 10 habitat types (Parker 1981*a*). Owing to movement patterns of collared lynx the study area was reduced in size during radio telemetry studies in 1979. To facilitate meaningful positioning of radio locations in 1979 the habitat was classified into five general types. Habitat types included mature conifer, mature mixed, early successional (5–15 years after cutting), advanced successional (16–30 years after cutting), and recent clearcut (≤4 years after cutting).

Snowshoe hares were livetrapped (double-door Tomahawk live trap; Tomahawk Live Trap Co., Tomahawk, Wisconsin) in various habitat types, ear-tagged (No. 3 monel metal
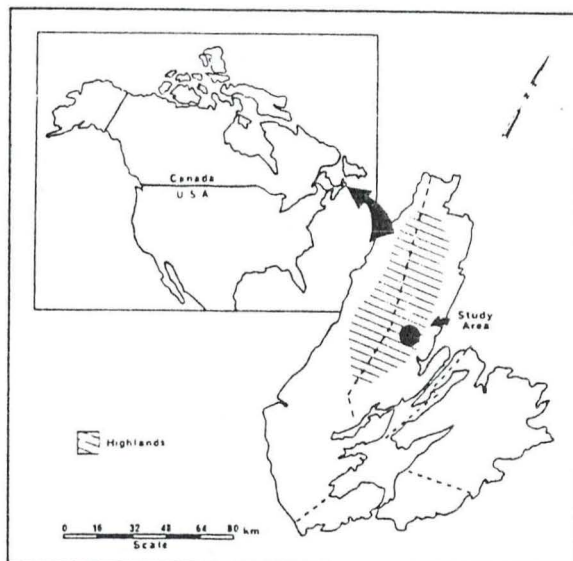

FIG. 1. Location of the Cape Breton Island study area.

eartags; National Band and Tag Co., Newport, Kentucky) and released in the summers of 1977, 1978, and 1979. Six sites trapped in 1977 were retrapped on the same calendar dates in 1978 and 1979 to provide an index of annual change in hare densities. Snowshoe hare densities were estimated in summer 1977 by the linear regression method, using capture frequency (Edwards and Eberhardt 1967).

In summer 1977, small mammals were sampled within four common habitat types. Victor snap traps, baited with a mixture of peanut butter and rolled oats, were placed at each 10-m interval along three parallel 90-m transects, each transect separated by 20 m. Each site was trapped for four consecutive nights (120 trap-nights). The number of trap sites per habitat type varied from one to four. Each site was trapped for only one four-night trapping period.

Lynx carcasses were collected from trappers from 1977–1978 through 1979–1980. Carcasses were weighed and measured (total length, tip of nose to last caudal vertebrae; metatarsus, length of the unskinned metatarsus bone in the hind leg; shoulder height, distance from tip of toe along radial surface of extended foreleg to dorsal tip of the spinous process of thoracic vertebrae). Three fat deposits were removed and weighed. Those deposits were (*i*) thoracic, the pad of fat attached to the posterior extension of the sternum; (*ii*) mesenteric, the fat attached to the folds of the mesentery and omentum; and (*iii*) abdominal, the fat attached to the dorsal side of the body cavity, from the anterior end of the kidneys posterior to the groin. An upper canine was removed and stored in 5% formalin. Young-of-the-year (kits) were identified by the open root apical foramen (Saunders 1964; Brand and Keith 1979). Teeth with closed root apical foramina were decalcified, sectioned, and stained after Parker (1981*b*). The method of determining the ages of lynx from stained tooth sections followed that of Crowe (1972) and Nellis et al. (1972). Stomachs were removed from lynx carcasses and frozen. Stomach contents were later washed over a fine-meshed sieve and prey species identified and weighed. Food

items were identified by comparison with skeletal reference material from the National Museum of Natural Sciences, Ottawa, a reference collection of known hair samples, and a reference avian collection at Canadian Wildlife Service, Sackville. Female reproductive tracts were removed and washed. The uterine horns were slit, the tissue was spread on a glass surface, and placental scars were counted over a light source.

To determine the influence of year of collection (three seasons: 1977–1978, 1978–1979, 1979–1980), month (November through March), age and sex on morphological measurements (carcass weight and length, metatarsus length, shoulder height), and indices of physical condition (abdominal, mesenteric, and thoracic fat weights), a five-way analysis of variance was used. The variables year, month, age and sex were considered to be the independent variables and the others, dependent. To analyze unbalanced data (i.e. varying numbers of observations per cell) with missing cells, the GLM procedure (Anonymous 1979) was used. To test for significant differences in a dependent variable between two levels of an independent one (e.g., whether lynx differed in weight between males and females), Bonferonni's test (Miller 1966) was used. The unbalanced nature of the data precluded more common multiple comparison tests.

It was impossible to test for all interactions and main effects simultaneously as this would result in more parameters than observations. Hence we considered only main effects and two-way interactions. A preliminary analysis of variance showed none of the interactions were at all significant (generally $p > 0.5$), hence we considered only the main effects. Further, animals of age 3.5 years or more were combined into a single "adult" category since a preliminary analysis of variance showed no difference in the dependent variables among these ages. After the above steps were taken, the effects of the remaining independent variables were investigated.

Lynx trails were followed on snowshoe in winter 1977–1978. The length of trail (metres) and activities (e.g., chases, kills, beds) within each habitat were recorded. Scats were collected while tracking lynx in the winter (1977–1978) and along roads and trails in the summers of 1977 and 1978.

Lynx were livetrapped in early winter 1978–1979 in padded Oneida No. 4 leg-hold jump traps, immobilized with ketamine hydrochloride (concentration, 100 mg/mL; 15.0 mg/kg body weight; available from Rogar/STB., London, Ontario), fitted with radio collars, and released. The intramuscular drug was injected by hand syringe into the hind quarters. Lynx were located by multiple bearings with hand-held yagi antennae and a TRX-24 receiver (Wildlife Materials, Inc., Carbondale, Illinois). Radio collars were prepared by Bioelectronics Section, Canadian Wildlife Service, Ottawa and frequencies were in the range of 150–151 MHz. The study area contained a good network of logging roads, thus facilitating travel by snowmobile in winter and truck and trail bike in summer.

Results

Population characteristics

Sex and age structure

One hundred fifty-four lynx carcasses were collected during the public trapping seasons from 1977–1978
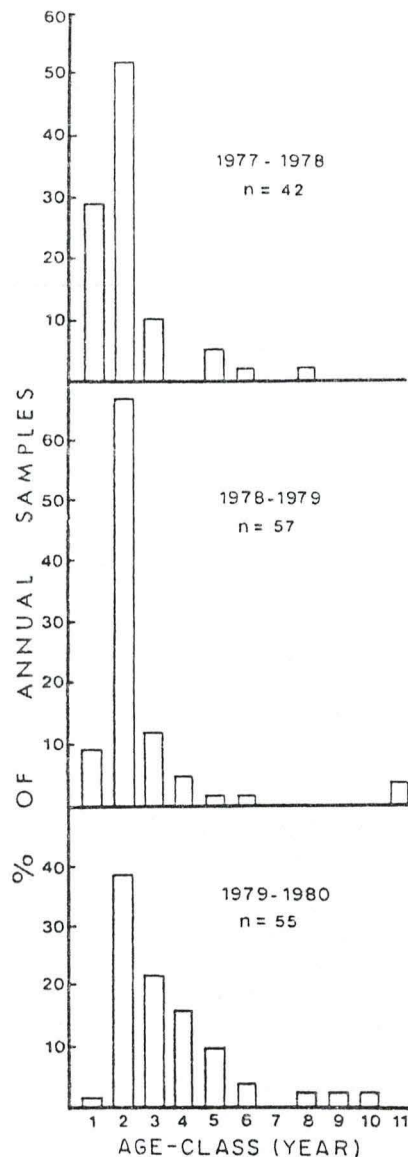

FIG. 2. Age structure of lynx harvested on Cape Breton Island from 1977–1978 through 1979–1980.

through 1979–1980. Annual male:female ratios were 68:32 (1977–1978), 51:49 (1978–1979) and 45:55 (1979–1980); the 3-year sample ratio was 54:46. Only in 1977–1978 did sex ratios differ from equality ($\chi^2 = 5.48$; $p < 0.05$).

The age structure[1] of the sample changed over the three year period (Fig. 2). The representation of kits (1 year) declined from 29% to 9% and 2% during those years ($p < 0.005$) while respective yearling (2-year) percentages were 52, 67, and 39% ($p > 0.05$). Kits and

[1]Integers are used for age assignment; i.e. $\frac{1}{2}$ year = 1; $1\frac{1}{2}$ year = 2; etc.

TABLE 1. The proportion of females with placental scars and the mean number of scars per breeding female for lynx harvested on Cape Breton Island from 1977–1978 through 1979–1980 (sample sizes in parentheses)

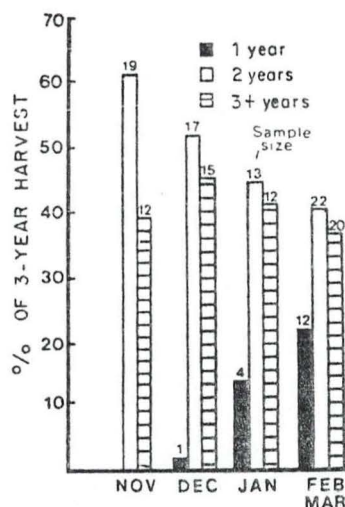| Age (years)	% females with placental scars			Mean no. of scars*		
	1977–1978	1978–1979	1979–1980	1977–1978	1978–1979	1979–1980
2	67(6)	29(14)	0(10)	3.7	2.7	—
3+	75(4)	71(7)	64(14)	3.3	3.8	3.8

*Between-year differences not significant ($p > 0.05$)

FIG. 3. Monthly changes in the age structure of lynx harvested on Cape Breton Island from 1977–1978 through 1979–1980.

yearlings together declined from 81% to 76%, and 41% over the 3-year period ($p < 0.005$). The oldest lynx were aged at 11 years. No more than 6% of the sample was older than 6 years in any year.

The composition of the three year harvests was examined by month (Fig. 3). The proportion of yearlings declined from November through February–March ($p > 0.05$) while the proportion of kits increased ($p < 0.001$). The representation of older lynx (3+ years) remained stable. More females than males were caught in November and December while the January and February–March samples favoured males ($p > 0.05$).

Reproduction

Twenty-seven percent of yearlings ($n = 30$) and 68% of older females ($n = 25$) in the 3-year sample had given birth the previous spring (placental scars present). Although the percentage of females 3+ years which had given birth declined over the period of study (75% in 1977–1978 vs. 64% in 1979–1980), the largest decline was the yearling age-class (67% in 1977–1978 vs. 0% in 1979–1980; Table 1). Although the mean litter size for yearling females declined from 1977–1978 to 1978–

1979, that decline was not significant ($p > 0.05$). Mean litter size for females 3+ years actually increased from 1977–1978 to 1979–1980.

Most female lynx reached reproductive maturity by their second breeding season (22 months). Although lynx conceived during their first breeding season (9 months) the reproductive success of those young females appeared to be dependent upon the abundance of snowshoe hares. Although high infant mortality may severely reduce recruitment, successful breeding by females 22 months or older appeared to be only slightly influenced by reduced numbers of prey.

Morphology and physical condition

Table 2 summarizes the results for seven analyses of variance, one for each dependent variable. Age influenced all physical and fat deposition measurements ($p < 0.01$). Sex influenced physical measurements ($p < 0.01$) but not fat deposition ($p > 0.40$). Month of collection influenced body weight and accumulation of mesenteric and thoracic fat ($p < 0.02$) while year of collection influenced only weight.

Carcass weight

Carcass weight was approximately 10% less than whole body weight. This was determined from a sample of pre- and post-skinning weights supplied by trappers. Adult body weight was reached at about 2 years by both males and females. Males were significantly heavier than females ($p < 0.0001$). The difference was most marked in the kit and yearling age classes (Fig. 4).

The body weights showed a significant decline from 1977–1978 through 1979–1980 ($p < 0.0001$). All ages and both sexes exhibited the same trend although in most cases there were not enough data to show differences within individual age or sex classes.

Month of collection influenced body weight. There was a decline in weight from November to January ($p < 0.018$) followed by an apparent increase from January to February ($p < 0.10$) (Fig. 5). The significance level on the increase is only 0.10 hence more study is needed to verify beyond doubt that the increase is real. However, a test for quadratic trend revealed that the weight at least levelled out after January.

Carcass length

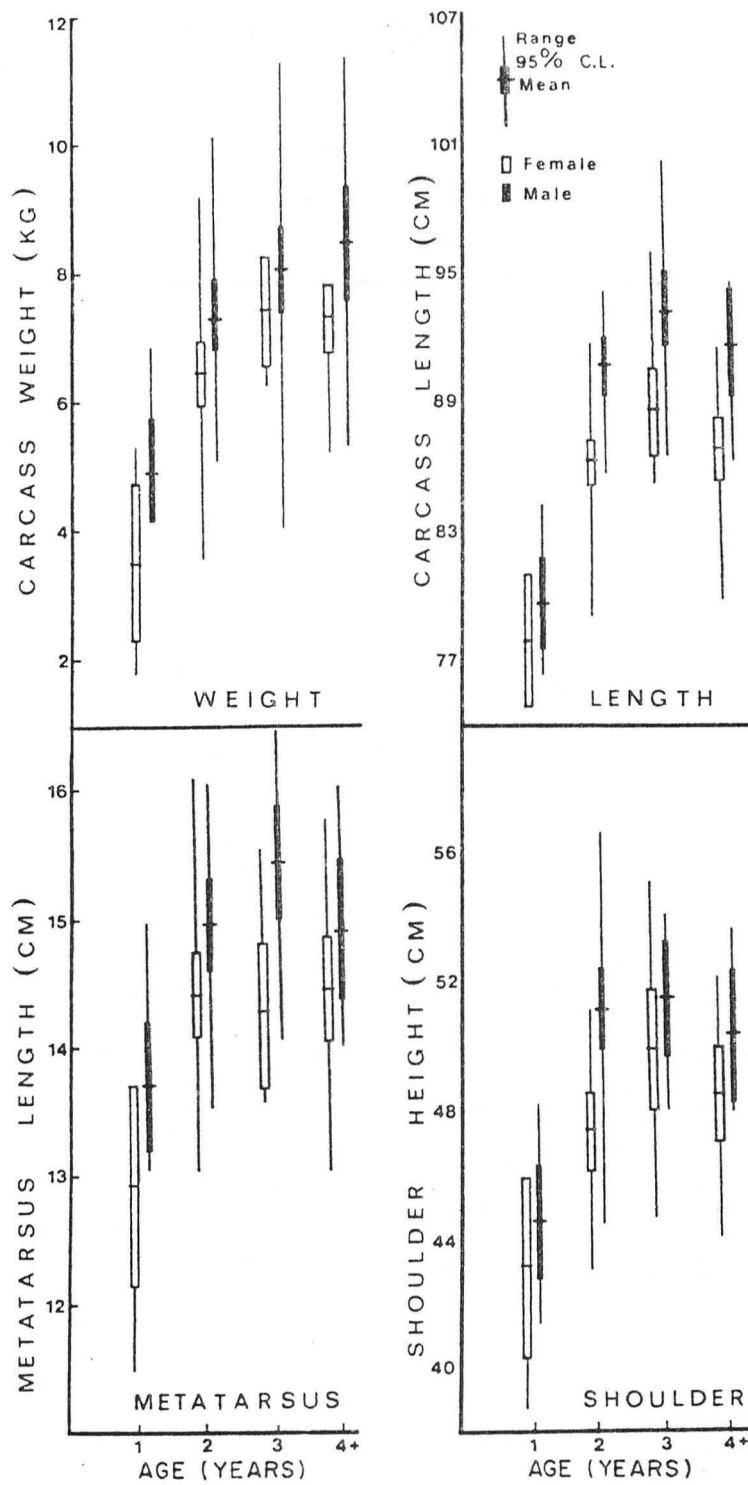Similar to weight, both sexes reached mature body

Fig. 4. Body weights and measurements of lynx harvested on Cape Breton Island from 1977–1978 through 1979–1980.

TABLE 2. The influence of year, month, sex, and age upon morphological and physical condition measurements of lynx collected on Cape Breton Island from 1977–1978 through 1979–1980 (SAS general linear models procedure; entries in the table are the type 1 errors, i.e. probability that the independent variable did not influence the dependent variable)

	Independent variable[a]			
Dependent variable	Year[b]	Month[c]	Age[d]	Sex
Carcass weight	0.0001**	0.0110*	0.0001**	0.0001**
Carcass length	0.2175	0.3924	0.0001**	0.0001**
Metatarsus length	0.2611	0.0696	0.0001**	0.0001**
Shoulder height	0.3231	0.2062	0.0001**	0.0001**
Abdominal fat weight	0.2420	0.0617	0.0057**	0.4059
Mesenteric fat weight	0.8336	0.0106*	0.0029**	0.9682
Thoracic fat weight	0.7450	0.0179*	0.0013**	0.6715

[a]Significance level ≤0.05.
[b]Years: 1977–1978; 1978–1979; 1979–1980.
[c]Months: November, December, January, February, March.
[d]Age: 1, 2, 3, and 4+ years.
*Significant at $p < 0.05$.
**Significant at $p < 0.01$.

length values by 2 years. Overall, males were significantly longer ($p < 0.0001$) than females. Bonferroni's test showed this difference was significant for each age class ($p < 0.02$) except the kits where it was not ($p = 0.30$).

Metatarsus

Both sexes reached mature values for metatarsal length by 2 years (Fig. 4). Metatarsal lengths of males were significantly greater ($p < 0.001$) than those of females. The greatest difference was in the 3-year age-class. There was little variation in metatarsal length once mature values were reached.

Shoulder height

Both sexes reached mature values for shoulder height by 2 years (Fig. 4). Shoulder height values for males were significantly greater ($p < 0.0001$) than those of females, the greatest difference being in the 2-year age-class. There was considerable variation in the shoulder heights of 3+ year age-classes for both sexes.

Fat deposits

Each of the three fat deposits (mesenteric, abdominal, and thoracic) increased with age ($p < 0.01$), at least to 4 years of age (Fig. 6). However, because of the great variability in fat among individual animals, increases were not significant except for the lower fat deposits in yearlings ($p < 0.05$). Month of collection influenced only thoracic and mesenteric fat deposits ($p < 0.05$). For both deposits, February measurements were greater than those of December ($p < 0.03$) and for mesenteric fat, February's fat deposits also exceeded January's ($p < 0.04$) (see Table 3). For all three fat deposits there was

an indication of declining reserves from November through December followed by an increase from January through February (Fig. 5).

Prey availability

Snowshoe hare

Snowshoe hare densities declined on the study area from 1977 through 1979. Live-trapping success (hares per 1000 trap nights) declined 73% over the 3-year period. Densities of hares varied among habitats sampled, although the relative abundance of hares among habitat types was similar in all 3 years. Hares were most frequently caught in open mature conifer habitat followed by advanced successional, early successional, and closed mature conifer types (3 years combined = 309, 146, 139, and 61 first captures per 1000 trap nights, respectively).

The distribution of hares among habitat types in winter changed from that of summer. The distribution of pellets stressed the importance of successional habitat to hares in the winter. Advanced successional habitat supported three times the densities of pellets found in the next important type, the closed mature mixed (Parker 1981a). The distribution of winter pellets may be related to the availability of hardwood browse (~7 stems/10 m^2; mean height = 2–3 m) and optimum conifer cover (~9 stems/10 m^2; mean height = 2.5–3.0 m) found in advanced successional habitat. Mature conifer provided suboptimal values for hardwood browse (~3 stems/10 m^2; mean height = 0.5–1.0 m) and conifer cover (~3 stems/10 m^2; mean height = 6–8 m).

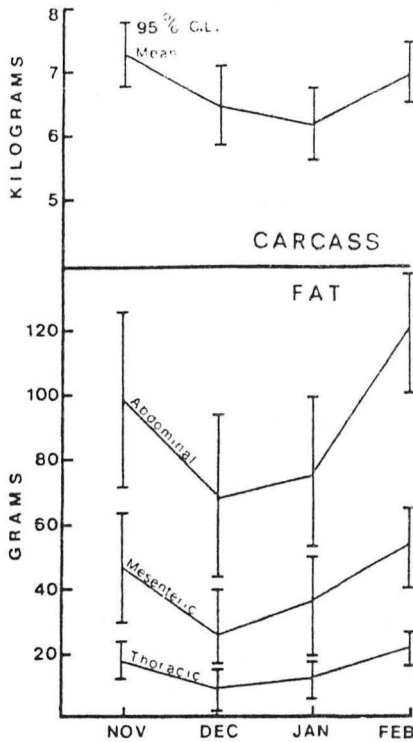Estimated densities of hares ranged from 1000/100 ha

FIG. 5. Changes in monthly fat depositions (weighted means, ANOVA) and carcass weights for lynx collected from November through February (March sample excluded due to small sample size), 1977–1978 through 1979–1980.

in advanced successional to 580/100 ha in mature conifer. A decline in hare densities over the three years reduced population levels in advanced successional from 1000/100 ha in 1977 to 170/100 ha in 1979.

Small mammals

The most common and ubiquitous small mammal on the study area was the red-backed vole (*Clethrionomys gapperi*), representing 84% of total specimens captured (Table 4). The next most abundant small mammal was the masked shrew (*Sorex cinereus*). Although seven species were represented in the overall sample, the red-backed vole and masked shrew accounted for 96% of total captures. Small mammals were most abundant in early regeneration (47% total captures), followed by closed mature conifer (36%), open mature conifer (10%), and late regeneration (7%).

Grouse

Ruffed grouse (*Bonasa umbellus*) and spruce grouse (*Canachites canadensis*) were common on the study area. No effort was made to estimate numbers or densities. Both species were seen regularly during summer and winter field studies, but neither was considered abundant during the period of study. Hunters and residents of the adjacent settlements were of the opinion that grouse populations were at or near a low
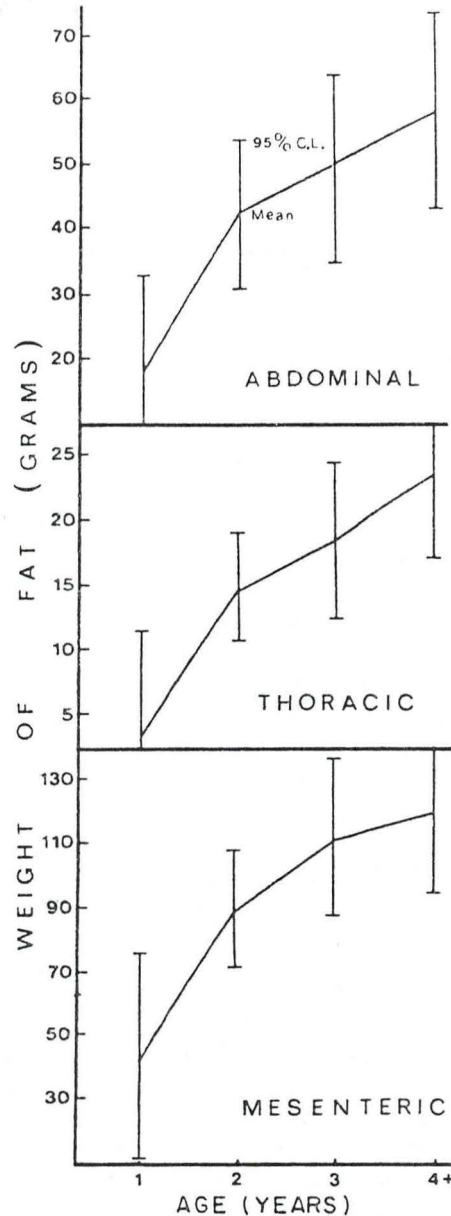

FIG. 6. Increases in fat deposits (weighted means, ANOVA) of lynx with age.

during the study, and our field observations supported that consensus.

Moose and deer

Moose (*Alces alces*) were distributed throughout the highlands and were common on the study area. We estimated 10–12 moose were within the study area distributed among four or five wintering yards.

Deer (*Odocoileus virginianus*) were only common on the study area when the ground was free of deep snow cover (May to December). In late November and early December, deer move down from the highlands and

TABLE 3. Bonferroni's test for significant relationship between fat deposits and month of collection (general linear models procedure, SAS package)

Month	Least squares means	Standard error		Bonferroni's test probability level			
				1	2	3	4
			Thoracic fat deposits				
(1) Nov.	17.1105	3.0728	1				
(2) Dec.	8.5465	3.2527	2	0.460			
(3) Jan.	11.1950	2.9871	3	—	—		
(4) Feb.	20.7213	2.1651	4	—	0.029	0.104	
(5) Mar.	17.6387	6.4697	5	—	—	—	—
			Mesenteric fat deposits				
(1) Nov.	99.5370	13.0506	1				
(2) Dec.	68.2909	13.8499	2	0.844			
(3) Jan.	74.8087	12.6491	3	—	—		
(4) Feb.	120.4059	9.3557	4	—	0.026	0.040	
(5) Mar.	90.7667	24.5991	5	—	—	—	—

TABLE 4. Success of small mammal trapping within common habitats on Cape Breton Island study area from July 6 to August 27, 1977

Habitat	Trap nights (TN)	Small mammals trapped*							Totals	Trapping success (mammals/100 TN)
		C.g.	M.p.	S.c.	P.m.	N.i.	Z.h.	B.b.		
Closed mature conifer	500	105		7					112	22.4
Open mature conifer	190	27		1		1	1		30	15.7
Late regeneration	371	19		7					26	7.0
Early regeneration	647	114	3	22	2			6	147	22.7

*C.g., Clethrionomys gapperi; S.c., Sorex cinereus; N.i., Napaeozapus insignis; B.b., Blarina brevicauda; M.p., Microtus pennsylvanicus; P.m., Peromyscus maniculatus; Z.h., Zapus hudsonius.

winter on the lower slopes and adjacent lowlands, moving back when the snow recedes in May.

Other mammals

Other mammals, or their signs, seen on the study area were red fox (*Vulpes vulpes*), otter (*Lutra canadensis*), mink (*Mustela vison*), weasel (*Mustela erminea*), black bear (*Ursus americanus*), red squirrel (*Tamiascuirus hudsonicus*), beaver (*Castor canadensis*), and bobcat (*Lynx rufus*). No interaction between lynx and any of these mammals was observed.

Feeding habits

Snowshoe hare was the most important component in the annual diet of lynx on Cape Breton Island (Table 5). The next most important food item was white-tailed deer, although only in summer scats did it surpass 5% occurrence. Ruffed grouse never exceeded 4% occurrence. The diversity of food items increased in summer, owing to the increased availability of small mammals and birds. The presence of deer in the winter samples can be attributed to bait and not predation (scats collected during snow tracking studies; lynx occasion-ally fed on deer bait from unsprung leg-hold trap sets). In summer, the presence of that species is believed to have come from the carrion of fall-shot or winter-starved deer.

Habitat selection

The use of different habitats by lynx based upon winter snow tracking studies in 1977–1978 has been reported by Parker (1981a). In 1979, 1506 locations of three radio-collared lynx (adult ♂; adult ♀; kit ♀) were plotted on cover type maps of the study area. The frequency of occurrences of collared lynx within specific habitat types were examined by χ^2 relative to the availability of those types.

All lynx were highly selective ($\chi^2 \geq 13.9$; df = 3; $p < 0.005$) at all seasons of the year although the adult female was more selective than the adult male or kit (Fig. 7). Selection for early and late successional habitat (all three lynx) and against mature mixed (adult ♂; adult ♀) during the winter period, supports results from snow tracking studies in 1977–1978 (Parker 1981a). In summer, use of successional habitat decreased and use

TABLE 5. Percent occurrence of food items in lynx stomachs (combined winter samples, 1977–1978 through 1979–80) and scats (winter 1977–1978; summers 1977, 1978)

Food item	Stomachs ($n = 75$)		Scats (% occurrence)	
	% occurrence	Weight (g)	Winter ($n = 55$)	Summer ($n = 441$)
Mammals				
Lepus americanus	97	104	93	70
Odocoileus virginianus	5	222	5	9
Clethrionomys gapperi	3	20	7	4
Tamiasciurus hudsonicus	1	21		4
Zapus hudsonius				<1
Birds				<1
Bonasa umbellus	3	tr	4	1
Perisoreus canadensis				<1
Unidentified birds			2	6
Fish bones				<1

of conifer habitat increased for both adults. Seasonal use of these habitats by the juvenile remained relatively constant.

Seasonal home range

Home ranges were larger in summer than in winter for both adults (Table 6). Summer range increases for the adult male and female were 108% and 73%, respectively. The home range of the juvenile was smaller in summer than in winter by about 22%. Based upon frequency of radio locations, lynx radiated out from central core areas in winter. Core areas were easily identified by plotting all radio locations on large scale maps of the study area. Core areas represented centers of lynx activity and are defined here as the central portion of a home range containing approximately 75% of all radio locations. Core areas represented 35%, 44%, and 63% of the winter home ranges of the adult female, adult male, and juvenile, respectively. Core areas could not be identified for summer home ranges.

The adult male and adult female shared the same winter home range (Fig. 8). In summer the male extended its range beyond that of the female (Fig. 9). Summer and winter home ranges for the juvenile were adjacent and discrete from those of the two adults. A small stream formed the boundary between those range limits and only on one occasion did the juvenile cross the stream and enter the adult home ranges; it returned after several hours. The adults were never known to cross the stream into the home range of the juvenile.

Daily movement pattern

Linear distances (metres) between 1040 paired radio locations were used to calculate daily cruising distances (DCD). Most paired radio fixes were separated by 1–2 h. No locations were used in calculating measurements of movement through time or distance if it was

probable that excessive meandering between fixes had occurred. Mean rates of travel (metres per hour) were calculated for each lynx by daily time period and season. Daily time periods were 0500–1000; 1000–1500; 1500–1700; 1700–2200; and 2200–0500. Time periods were chosen to best represent discrete periods of lynx activity, i.e. early morning, midday, late afternoon, evening, and night.

Daily cruising distances were greater in summer than in winter (Table 7). The female travelled more than the male and juvenile at all seasons. As calculated DCD's were sums of linear distances between consecutive radio fixes, true DCD's would be slightly greater because of unmeasured meandering travel between fixes. We subjectively estimated that the unmeasured distance travelled per day by all three lynx was approximately 1 km. Winter DCD's for the female, male and juvenile were estimated at 8.8, 7.6, and 6.5 km, respectively. Respective midsummer DCD's were 10.0, 9.5, and 7.2 km. Spring and autumn DCD's remained relatively constant for the female, but were lower for the male and juvenile.

As the seasonal DCD's for the three lynx suggest, the female normally travelled at a greater rate of speed (metres per hour) than the male, which in turn moved more rapidly than the juvenile (Fig. 10). In winter, all lynx travelled most rapidly during midday and early evening (1000–1700) followed by a decline during the night period (1700–0500).

In summer, activity patterns were less clear. The adult female was least active during midday, and very active in the late afternoon – early evening period, followed by reduced travel during the night. The male was most active from early morning through midday, least active during late afternoon, with increased activity throughout the evening and night periods. The juvenile showed no
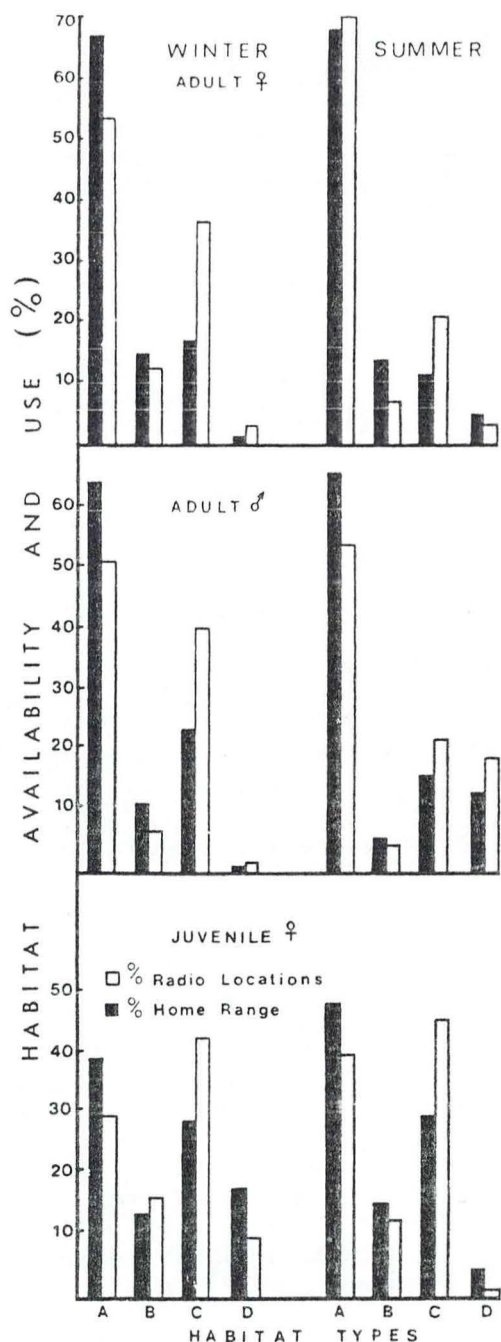
FIG. 7. Measure of seasonal habitat use by radio-collared lynx on Cape Breton Island, showing the percentage of radio locations by habitat type relative to availability of type (percent home range). Habitat types: A, mature conifer; B, mature mixed; C, successional; and D, recent clear-cut.

marked periods of activity, although it was most active during early morning and least active during midday.

Lynx travelled more diurnally in both winter and summer. The adult female, adult male, and juvenile

allocated 58%, 50%, and 56% of mean DCD, respectively, to the diurnal period. In summer, these figures increased to 74%, 74%, and 70%, respectively.

Hunting activities

During snow tracking studies in winter 1977–1978, 198 of 200 chases, and 34 of 36 kills were of snowshoe hares (Parker 1981a). Hunting success (percent successful chases) increased through the winter (January, 14%; April, 26%) and with group size (hunting success by groups of one, two, three, and four lynx = 14%, 17%, 38%, and 55%, respectively). A group of lynx usually represented a female with young, although occasionally a second adult would travel short distances with maternal groups (e.g., in winter 1979–1980, the radio-collared adult male often met and travelled with the radio-collared adult female and her three kits).

Distances between kills for groups of one, two, three, and four lynx were 7.6, 4.9, 2.9, and 0.5 km, respectively. Based upon frequency of kills (kills per kilometre of trail) by group size, and assuming a kill rate of one hare per lynx per 24-h period, it was estimated that lynx of all group sizes had a mean DCD of approximately 8 km during the winter of 1977–1978 (Parker 1981a). Monitored radio-collared lynx during the winter of 1978–1979 supported the estimated 8-km DCD in 1977–1978 by lynx of all group sizes (adult ♀ with three kits = 8.8 km; adult ♂ = 7.6 km; juvenile ♀ = 6.5 km).

Increased hunting success with group size was attributed to a cooperative hunting pattern, especially as kits developed and improved their hunting skills through the winter, a factor which we also attributed to the overall increased hunting success from January through April. When travelling through habitat where prey was scarce (e.g., mature conifer), a group of lynx often travelled single file, each stepping in the tracks of the lynx ahead. When moving through habitat where prey was abundant (e.g., successional), groups normally dispersed, each lynx travelling in the same direction, with trails zigzagging, meeting, and separating frequently. A hare chased by one lynx was often caught by another.

Grouse was found to be a minor component of the winter diet during snow tracking studies which agreed with results from stomach and scat analyses. Only 2 of 200 chases were of grouse; both, however, were successful and the result of chance encounters between travelling lynx and grouse in subniveal roosting forms.

We suggest that the travel and activity patterns of lynx, especially in winter, are primarily a function of hunting success. Well-used beds were normally associated with each kill. Radio-collared lynx were often stationary for several hours in the early evening, the time of day normally identified with rapid travel. It is reasonable to assume that those lynx had made an early kill. Other lynx travelled throughout the night and were

TABLE 6. Seasonal home ranges of radio-collared lynx on Cape Breton Island. 1978–1979

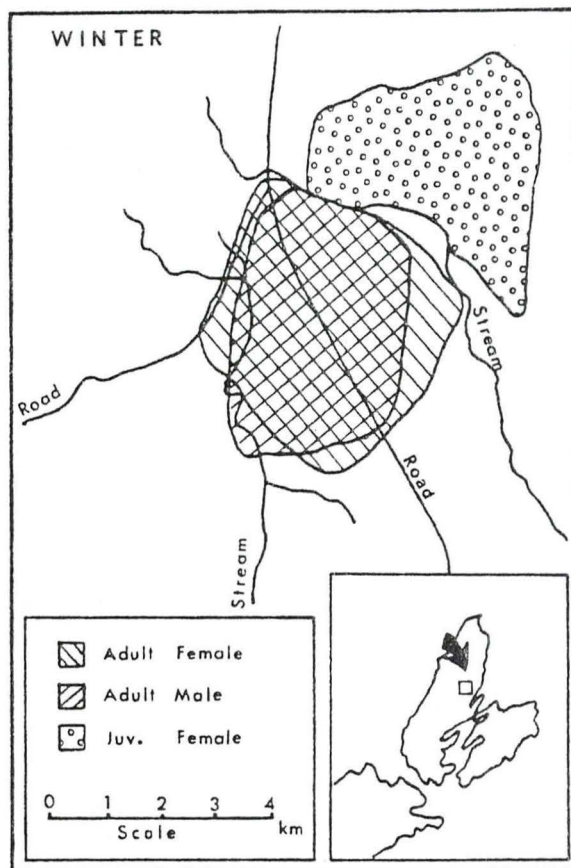| Collared lynx | Season | Home range (km²) | | Maximum diameter (km.) |
		Core area	Total	
Adult ♀	Winter	6.6	18.6	5.9
	Summer		32.3	7.3
Adult ♂	Winter	5.3	12.3	5.4
	Summer		25.6	9.9
Juvenile ♀	Winter	6.4	10.1	4.7
	Summer		7.9	5.6

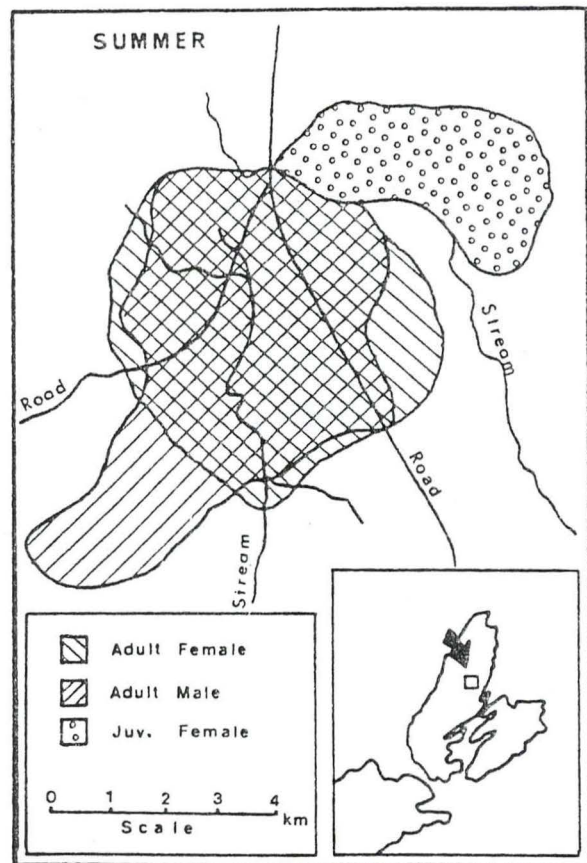FIG. 8. Home range limits of radio-collared lynx in winter 1980.

FIG. 9. Home range limits of radio-collared lynx in summer 1980.

apparently unsuccessful at making a kill. An early kill was followed by a period of inactivity. We believe that the length of inactivity following a kill depended upon group size and time since the last kill. A single lynx feeding alone might spend much of the night at the kill, while groups of three or four lynx would continue to hunt after a relatively brief period of feeding and rest. This scenario is compatible with documented group size specific rates of hunting success, rates of travel, and daily cruising distances.

The remains of kills varied from only skin, viscera, and paws to nearly intact carcasses. We interpreted the extent of prey use as a function of time between kills, especially for single lynx. An early evening kill might be totally consumed (except for unpalatable portions such as skin, paws, viscera, and the front portion of the skull containing incisors). After resuming travel later in the night that lynx might make a second kill, the carcass of which would receive only minor use.

In summer, information on hunting activities was

TABLE 7. The seasonal daily cruising distances (kilometres per 24-h period) for radio-collared lynx on Cape Breton Island from January to November 1980. (1 km added to each calculated DCD to account for unmeasured meandering between radio locations)

Collared Lynx	Season			
	Spring	Summer	Autumn	Winter
Adult female	8.91	10.06	9.06	8.82
Adult male	5.14	9.51	6.55	7.60
Juvenile female	6.00	7.27	4.55	6.51

limited to telemetry and analyses of scats. The greater diversity and abundance of prey reduced the more regimented pattern of daily activity adhered to during the winter. Scat analysis showed less dependency upon snowshoe hare in summer. Lynx became less dependent upon one large meal a day and varied their diet with birds, small mammals, and carrion.

Discussion

We identified a minimum of 11 lynx within approximately 60 km² during telemetry studies in the winter of 1978–1979 (2 adult ♂♂; 2 adult ♀♀; 6 kits; 1 adult unknown sex). This represented 18 lynx/100 km², and is based only on confirmed lynx identities. We suggest 20 lynx/100 km² was nearer the actual population density.

Thirteen lynx were removed from this area during public trapping the following winter (1979–1980). Assuming the population remained stable between years, trapping removed 65% of the 1978–1979 population. As pointed out earlier, the estimated density and mortality rate of lynx on the study area is not considered representative of that on the highlands in general. It does, however, illustrate the susceptibility of lynx to trapping in areas of high density and high trapping pressure.

Population densities over an 8-year study on a 130-km² area in Alberta ranged from 2.3/100 km² to 10.0/100 km² (Brand et al. 1976) and maximum densities in forested regions of the Central Zone of the U.S.S.R. have been estimated at 5.0/100 km² (Iurgenson 1955). Densities in this study were twice the maximum densities reported in Alberta and four times those reported from the U.S.S.R.

The change in age structure of the monthly harvests for November through February–March is interesting from a management perspective. Although yearlings remained the largest single cohort in the monthly samples, the proportion of yearlings declined from 60% in November to 40% in February–March. Yearlings, lacking the protection and experience provided by the adult female the previous winter, are most prone to
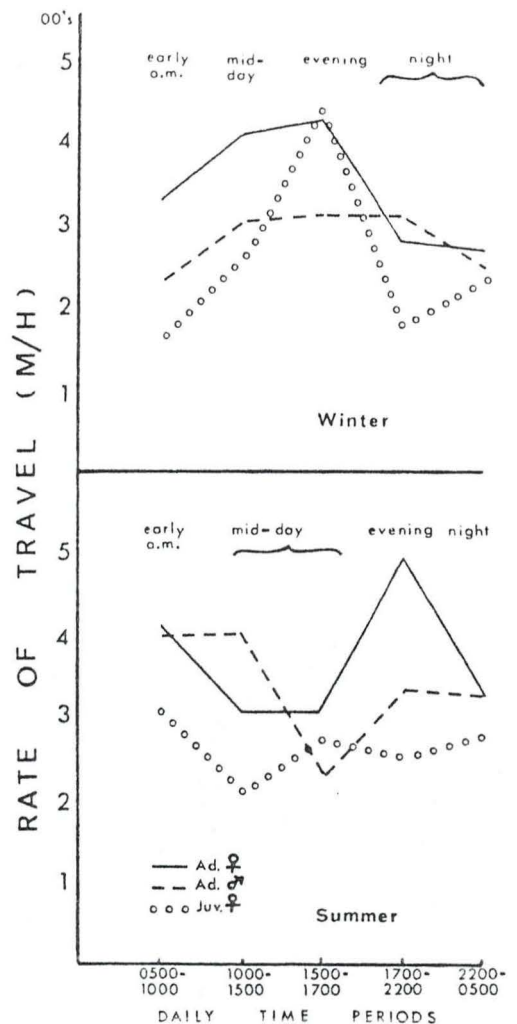

FIG. 10. Seasonal daily rates of travel (metres per hour) for radio-collared lynx.

being caught. The representation of yearlings in the monthly harvests declined relative to their removal from the population. The representation of lynx 3 years old and older remained relatively constant throughout the winter. The most marked change in monthly age-class representation was within the 1-year cohort; from 0% in November (n = 31) to 22% in February (n = 54). The proportions of kits in the December and January samples were 3% and 14%, respectively. We suggest that as adult females with young are removed from the population through the winter, an increasing number of kits became orphaned and are very susceptible to being trapped.

A shortened season would reduce the proportion of kits in the harvest. A later season (January–February) would allow orphaned kits the added benefit of being several months older with winter hunting experience learned from the female in November and December.

Kits orphaned in January and February would be more able to hunt for themselves than those orphaned in November and December. A later season also benefits from increased pelt primeness and subsequent fur value.

Mean litter sizes are lower than those reported for lynx in Alaska (Nava 1970) and Alberta during periods of hare abundance (Brand and Keith 1979) but comparable to lynx in Alberta when hares were moderate to low in abundance (Brand and Keith 1979).

The decrease in recruitment (i.e., decline of kits in harvest) over the 3-year study resulted from a reduction in the breeding rates of adult females, a virtual cessation of breeding in yearling females, and an apparent high rate of infant mortality within litters by females which did breed successfully. The decline in rates of breeding and recruitment coincided with a decline in the abundance of snowshoe hares. These results are in agreement with those from Alaska (Berrie 1974) and Alberta (Brand and Keith 1979) where similar changes in the age structure and recruitment of lynx populations occurred during reductions in the availability of snowshoe hare.

A decline in carcass weights (weighted means) from 1977–1978 through 1979–1980 coincided with a decline in snowshoe hares. No single physical or morphological factor could be isolated that significantly influenced between-year declines in weight, although most physical measurements were less in 1979–1980 than in 1977–1978. Weighted measurements of body length, girth, shoulder height, metatarsus length, and the weight of two of three body fat reserves were all less in 1979–1980, although none of the individual differences were significant.

We suggest that the sum of statistically insignificant declines in individual physical and morphological parameters was sufficient to produce significant between-year decreases in body weight. We further suggest that temporal declines in physical and morphological parameters were a response to a decrease in the density of snowshoe hares over the same period.

Male:female ratios for the 3-year sample show a trend from a preponderance of males in the kit age class to equality in the adult class (kits = 65 ♂ ♂ : 35 ♀ ♀, $n = 17$; yearlings = 57 ♂ ♂ : 43 ♀ ♀, $n = 70$; adults = 50 ♂ ♂ : 50 ♀ ♀, $n = 60$). Although sex ratios favouring males have been reported from Alaska (Berrie 1974), Alberta, and the Northwest Territories (van Zyll de Jong 1963) and Ontario (Stewart 1973), Brand and Keith (1979) could find no significant deviation from a 50:50 ratio in lynx from Alberta for age-class, hare abundance, or season. They suggested deviations may reflect sex specific trap biases and this may well apply to the Cape Breton Island sample.

The three body fat reserves were closely related (Spearman rank correlation, $r_s > 0.8$). Fat reserves declined in early winter but increased in January through

February. Although those changes were significant ($p < 0.001$), the mode of change is difficult to explain. A gradual loss through the winter was expected; the increase late winter was not. The observed monthly decline and then increase may have several possible explanations.

Yearlings comprised the largest age cohort in all monthly samples. Following an initial loss of fat (December) owing to poor hunting skills in early winter, hunting success improved and fat reserves increased with experience gained through the winter. Another possibility is that when the first snow cover accumulates (December) and hunting becomes more difficult those lynx in the poorest physical condition (lowest fat reserves) are prone to be trapped first. Lynx in the best physical condition are the last to be trapped (February).

The fluctuation in monthly body weight was very similar to the weight of body fat reserves (Fig. 6). Spearman rank correlations were calculated between weight and each fat reserve for each age–sex category. All were found to be positive. Where there were sufficient observations to make the test sufficiently powerful, most correlations were significant. This supports what we would expect since the factors influencing body weight are similar to those previously mentioned for monthly fat reserves.

We suggest that trapping can be a major source of mortality on lynx ≥1 year of age. The study area was closed to public trapping during radio telemetry studies in winter, 1978–1979. The area was reopened to trapping on November 1, 1979. All marked lynx were killed by hunters or trappers in the early winter of 1979–1980, and all within 1 km of where they had been live-captured and released approximately 1 year earlier.

The type and intensity of mortality on lynx ≤1 year of age appears dependent upon the availability of snowshoe hares. When hares are abundant, natural mortality on kits is low, fall recruitment rates are high, and kits constitute a large proportion of the harvest. When hares are scarce, kits experience a high rate of infant mortality prior to the fall trapping season, fall recruitment rates are low, and kits make up a small proportion of the harvest. This scenario is similar to that for lynx populations in Alaska (Berrie 1974) and Alberta (Brand and Keith 1979).

The collared female showed no activity changes through the spring and summer of 1979 to suggest that it had successfully given birth to, or was caring for, a new litter of lynx. At point of death in November, however, four placental scars confirmed that she had successfully bred the previous spring. The lack of any detectable change in daily activity patterns suggests that the young were dead at birth or died shortly thereafter. The virtual absence of kits in the fall harvest, in spite of continued breeding by a high proportion of adults (from placental

scars) suggests the fate of that particular litter probably represents that of most other litters born during periods of low food availability.

In this study lynx were found to be selective in their use of habitat types within defined home range boundaries. Winter tracking and radio telemetry showed lynx selected for regenerating mixed forest habitats approximately 20 years following cutting. Forest stands of this type also represented optimal habitat for snowshoe hares.

Lynx depended upon close approach to prey for maximum hunting success; these conditions were best satisfied in the advanced successional and closed conifer habitats. Hunting success appeared more dependent upon hunting conditions (i.e., optimum cover for close encounters with hares) than upon hare abundance.

Optimum lynx habitat on the highlands of Cape Breton Island was represented by a mosaic of approximately 50% mature conifer, 30% mature mixed, 12% successional (~20 years following cutting) and a scattering (~8%) of peat bogs, alder swales, and small streams and ponds. We suggest that the amount of successional habitat could have been increased to 20–25% at the expense of the mature mixed type.

The creation of successional habitat through forest harvesting and wildfires improves habitat for snowshoe hares and ultimately for lynx (Burris 1971; Nellis 1971). Relative to the extensive harvesting of the mature balsam fir forests on the highlands of Cape Breton Island and the time lapse (~15–20 years) before optimum mixed successional habitat regenerates, the short-term impact of the loss of that habitat to lynx is uncertain. Clear-cutting operations remove the conifer cover from large tracts of land. It is not known if lynx would use all of the successional habitat available following regeneration or only those portions within a maximum threshold distance from mature conifer forest.

The productivity of the lynx population on Cape Breton Island, and throughout the range of lynx in North America, is closely associated with the cyclic abundance of snowshoe hares. From Newfoundland to Alaska snowshoe hare is the principle component in the diet of lynx (Saunders 1963; van Zyll de Jong 1966; Nellis and Keith 1968; Nellis et al. 1972; More 1976; Brand et al. 1976; Brand and Keith 1979).

In this study the remains of snowshoe hares were found in virtually all stomach samples (those which contained food remains) and scats collected in the winter months. Dependency upon snowshoe hares declined in summer although hares remained the single most important prey species. A decline in the importance of hares and a greater representation of small mammals and birds in the summer diet of lynx concurs with the results of other feeding habit studies (Saunders 1963; van Zyll de Jong 1966; Nellis et al. 1972). The presence of deer in

winter scats came from trailed lynx which had eaten deer at trap stations. Deer were rare on the study area in winter; most had moved down the slopes to winter on the lowlands. The collared adult male lynx spent extended periods of time feeding and resting at the site of a deer carcass in early spring. We believe the deer had either been killed and lost by hunters the previous fall or had died from starvation during the winter. The presence of deer hair in summer scats may have been from carrion or predation. Lynx kill caribou in Newfoundland (Saunders 1963) and have been reported to successfully kill mule deer (*Odocoileus hemionus*) (Sheppard 1960). We suggest that the importance of lynx as a predator on deer on the highlands of Cape Breton Island is minor and most remains of deer in stomachs and scats are from bait or carrion.

There was no evidence of moose in lynx stomachs and scats although moose were common in the study area. In Newfoundland moose constituted 71% of the volume of lynx stomach contents from fall samples (Saunders 1963); the author attributed the presence of moose to carrion from hunter-killed animals. There was no hunting of moose on Cape Breton Island during this study.

In this study the mean daily cruising distance of 8 km/24 h by lynx during winter compares well with lynx cruising distances reported from Newfoundland (8.0 km, Saunders 1963) and Alberta (8.8 km in 1967, Nellis and Keith 1968). The estimated kill rate of one hare per 24 h, however, is twice the rate reported in those studies. Estimates of winter kill rates should be calculated by group size and through time (i.e., by month) as both influence hunting success. Increased hunting success through the winter probably resulted from improved individual hunting skills, although, as suggested by Nellis and Keith (1968), increased bearing strength of the snow may also contribute to hunting success.

Although we found it difficult to interpret the precise sequence of chase and kill for groups of three and four lynx, we believe that kits were actively participating in the hunt as early as January. Although the individual hunting skills of kits may have been less than those of adults, the cooperative hunting pattern of "fanning" through areas of high hare density increased the chances of hares being flushed and caught by one or more of the group. We suggest that the extent of participation in winter hunting by kits is dependent upon the age and development of the kit, factors related to variable parturition dates.

Other factors to consider when evaluating hunting success include group composition and age structure of the population. Groups of three and four lynx normally represent a female with kits. Two lynx travelling together may represent yearlings or, later in the winter,

an adult male and female. When recruitment rates are high (i.e., abundant food supply) many single tracks may be those of yearlings; during years of low recruitment (low food supply) most single tracks would be those of adults. We suggest that the hunting skills of single adults would be greater than those of single yearlings. Also, when a population is being heavily harvested, many single tracks may be those of kits which have lost their mother through trapping. Hunting success by orphaned kits would be very low.

The high hunting success rate of 42% for lynx in Newfoundland (Saunders 1963) applied to a female with two kits and two separate adult males. A high hunting success rate for those lynx would be expected. Brand et al. (1976) determined hunting success rates for lynx in Alberta for six winters of known hare densities. Success rates varied from 9% to 36%. They found no relationship between hunting success and hare densities. They did not, however, evaluate hunting success rates by group size or age structure of the population.

Management implications

The lynx on Cape Breton Island are isolated from mainland populations and restricted in distribution to the western highlands. Although the Cape Breton Highlands National Park represents a preserve which should ensure the continued survival of the species on the island, lynx outside the park are subject to potential overharvest and habitat change from extensive clearcutting operations.

Following several years of closed season, trapping of lynx was allowed in 1977–1978 on a quota basis of two lynx per licensed trapper. The season remained open through 1979–1980. The annual harvest showed little change over the 3 years although the age structure shifted towards older lynx. The change in the age structure and a decline in snowshoe hares prompted a closure of the season in 1980–1981 which was continued through 1982–1983.

Recruitment declined in response to a decrease in the availability of hares. The natural decrease in lynx densities can be sharply intensified by continued mortality from trapping. The population dynamics of lynx on Cape Breton Island are similar to those for populations in other regions of North America; the potential for delaying or suppressing natural increases in lynx populations by continued harvesting during periods of low recruitment has been emphasized by Brand and Keith (1979). On Cape Breton Island, where lynx habitat is limited and immigration from unexploited populations minimal (e.g., Cape Breton Highlands National Park), the importance of strictly regulated harvests is critical. Controlled harvest levels, as in 1977–1978 through 1979–1980, should be limited to years of high population recruitment. This can be regulated through the monitoring of snowshoe hare

densities (e.g., permanent winter track transects; summer livetrapping) and the sex and age structure of the annual lynx harvest. Harvest can be further regulated by the controlled issue of a special license.

There are two other potential threats to the future of lynx on the island: (*i*) the clearcutting of the mature conifer forest on the highlands, and (*ii*) the immigration and dispersal of the bobcat (*Lynx rufus*) throughout the lowlands over the past 25 years (the bobcat first appeared on the island shortly after the causeway was completed in 1955).

This study showed the importance of successional habitat to lynx. There has been no program to integrate forest harvesting and wildlife management on the highlands of Cape Breton Island. Clear-cutting is the prevalent method of tree removal, and the urgency for wood salvage necessitated by the widespread infestation of the spruce budworm has led to rapid and extensive loss of the mature conifer forest. Although this study emphasized the importance of successional habitat for the maintenance of high densities of lynx, the impact on lynx from the rapid replacement of mature conifer by extensive tracts of early successional (≤15 years) habitat is uncertain. Although early successional habitat may be used by hares in summer, deep snows cover the young conifers (≤2 m) in winter and leave little or no cover for hares. Large-scale forest harvesting operations on the highlands are nearly complete; it is now too late to integrate measures which would mitigate the loss of mature conifer forest (e.g., reduced size of clear-cuts; interspersion of uneven-aged cuts and mature conifer stands). We suggest that the short-term impact on lynx may be reduced densities in specific areas but in the long-term a general increase in the food and cover requirements of hares should result in increased densities of both hares and lynx.

Prior to the ingress and colonization of bobcats throughout the lowlands of Cape Breton Island in the past 25 years, lynx were common over much of the island. Concurrent with the colonizing of the lowlands by bobcat, lynx densities declined until they are now common only on the highlands, the one area where bobcats have yet to become established.

Whether the decline in lynx densities was coincidental with the dispersion of bobcats or a direct result of that phenomenon is uncertain. We suggest that deep winter snow cover is the reason bobcats have not yet colonized the plateau. In the winter of 1977–1978, snow depths on the study area were ≥75 cm from January through March. At Sydney Airport on the lowlands, end-of-the-month snow depths for January, February, and March 1978 were 1, 13, and 0 cm, respectively (Canadian Weather Review, Environment Canada, Ottawa). Although the lowlands normally have greater snow accumulation than that of 1977–1978 (1978–1979 and 1979–1980 were also years with low snow accumula-

tion), the 1977–1978 comparison does indicate the greater snow depths on the highlands relative to the remainder of the island.

In March 1979 we tested the relative supporting capacity of lynx and bobcat paws in snow. A snow pit was dug and, using an NRC snow kit, horizontal hardness was measured at 150 g/cm². Lynx and bobcat paws, taken from carcasses returned by trappers, were then secured to the snow hardness gauge, replacing the standard discs. Pressure was applied until the paw broke through the surface. A series of measurements were taken for three adult lynx and five adult bobcat forepaws. The mean readings of bobcat and lynx paws were 22 (range = 20–25; s = 2.7) and 43 (range = 40–50; s = 5.7), respectively ($p < 0.01$). Lynx paws, because of greater surface area, supported approximately twice the weight of bobcat paws. Adult male bobcat on Cape Breton Island average 40% heavier than adult male lynx (G. R. Parker, in press). Whereas deep winter snow presents little obstacle to lynx, bobcats would experience considerable difficulty in travel and capture of prey.

Lynx harvest regulations should be flexible and ensure that the annual sample is examined for sex and age structure. A quota system similar to that introduced from 1977–1978 through 1979–1980 should serve as control against overharvest. A closed season should be considered during periods of low hare densities and suppressed lynx recruitment. Management strategies can benefit from time- and age-specific mortality rates. A shortened season not only reduces the numbers of lynx harvested but changes the age structure of the harvest. The proportion of kits in the harvest increases with length of season while the proportion of yearlings decreases. Representation of older lynx remains relatively stable. When recruitment rates are high, a delayed season (January–February) would ensure a high proportion of yearlings and a low proportion of kits in the harvest. Kits orphaned in late winter would have a greater chance of survival than those orphaned in November and December.

A forest management plan which incorporates the habitat requirements of snowshoe hares is in effect a management plan for lynx. A forest of diversified tree and shrub species and stand age represents optimum hare and lynx habitat. The future of the lynx on Cape Breton Island appears secure although limited within the prescribed confines of geography and the cyclical nature of the species.

Acknowledgements

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LYNX

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The Canada lynx (*Felis lynx*) and its close relative the bobcat (*F. rufus*) are the most common wild felids of Canada and the United States respectively. A strikingly beautiful furbearer, the lynx is an important component of the wild fur industry, contributing significantly to the income of trappers in the Far North. The famous "10-year" population cycle of the lynx has long fascinated naturalists and wildlife researchers.

The lynx, generally considered a rare animal because of its secretive nature, is actually quite common throughout most of its North American range, which encompasses the vast boreal forests of Canada and Alaska. The advent of the snowmobile, which opened remote areas to trapping, combined with an unprecedented increase in the value of lynx pelts during the late 1970s, has greatly increased trapping pressure on the lynx. This has concerned wildlife managers and has stimulated research into establishing a firm biological basis for management.

DESCRIPTION

The lynx and bobcat arose from a common ancestor, although paleontologists are uncertain of its identity (R. L. Peterson, pers. commun.). The two species possibly are the result of separate invasions of the Asian lynx (*F. lynx lynx*) across the Bering Land Bridge during interglacial periods of the Pleistocene (the Asian lynx today is nearly twice the size of *Felis lynx* and looks more like a bobcat). This intriguing theory has the first immigrant population of Asian lynx evolving independently during the period of geographic isolation (perhaps 20,000 years) and eventually establishing a distant "southern" cat that became the bobcat; the second invasion of Asian lynx then filled the niche left by the retreating glacier and in turn underwent speciation as the North American lynx.

The classification of the lynx is disputed. Some taxonomists argue that the lynx and the bobcat are not sufficiently distinct from cats of the genus *Felis* to deserve a separate designation (Van Gelder 1977). The question is unresolved and still debated among taxonomists.

The species is remarkably homogeneous considering the widespread distribution of lynx in North America. There are only two recognized subspecies and one is confined to insular Newfoundland (McCord and Cardoza 1982). Several subspecies exist in Eurasia, including one isolated in Spain and considered endangered (McCord and Cardoza 1982). Hybridizations of lynx and bobcats are unknown; any that occur must be rare (R. L. Peterson, pers. commun.).

The lynx is a medium-size, reddish to gray-brown cat with relatively long hindlegs, which give it a stooped posture. Lynx are not nearly as big as they appear; long legs and dense fur exaggerate the size of the body, and adult males weigh only about 10 kg (22 pounds) (Table 1). Adult female lynx are somewhat smaller, averaging about 8.5 kg (19 pounds). The total length (head to tail) of adult male lynx is about 85 cm (33.5 inches), females 82 cm (32 inches). Although essentially full-grown by their second winter, lynx do not attain full adult weight until their third winter. Kits (young of the year) grow rapidly but are about 15 cm (6 inches) shorter than adults in winter (Quinn and Gardner 1984).

Table 1. Mean body weights (kg) and lengths (cm) of lynx in various North American regions ($\bar{x} \pm$ SD).

	Kits		Yearlings		Adults		Source
	M	F	M	F	M	F	
BODY WEIGHT							
Newfoundland					10.6 (range 6.3–17.2)	8.5 (4.9–11.7)	Saunders (1963)
Alaska	6.8 ± 0.7	5.1 ± 0.2	9.2 ± 1.4	7.9 ± 1.0	9.9 ± 1.4	8.8 ± 1.0	Nava (1970)
Cape Breton Island	6.4 ± 0.8	4.7 ± 0.6	9.0 ± 1.6	7.2 ± 1.1	9.1 ± 1.6	8.0 ± 1.2	Parker et al. (1983)
BODY LENGTH							
Newfoundland					89.2 (range 73.6–106.6)	84.3 (76.2–96.5)	Saunders (1963)
Ontario	68.5 ± 5.3	67.3 ± 5.0	83.7 ± 3.8	80.5 ± 2.9	85.2 ± 3.2	81.2 ± 3.0	Quinn and Gardner (1984)
Manitoba	70.0 ± 3.1	67.4 ± 3.1	79.5 ± 3.5	76.5 ± 3.0	83.5 ± 3.0	80.5 ± 2.5	Koonz (1976)
Alaska	71.2 ± 9.0	70.0 ± 4.6	83.4 ± 5.5	79.7 ± 3.0	87.0 ± 3.7	82.1 ± 2.7	Nava (1970)
Cape Breton Island[a]	69.6 ± 2.1	66.9 ± 1.4	79.4 ± 2.2	74.8 ± 2.9	80.2 ± 3.8	76.2 ± 2.8	Parker et al. (1983)

The winter pelage is a grizzled, grayish brown mixed with buff or pale brown. The belly, legs, and feet are grayish white or buff white. It is this light fur of the underparts that makes lynx pelts so valuable. The belly fur, particularly that of kits, is selected to make top-quality garments. Lynx molt the winter coat during late spring and acquire a darker, reddish brown pelage.

The lynx as a species is relatively undiversified morphologically. No prominent geographic color variants exist in North America. Occasionally, the so-called "blue lynx" is captured. This is a rare color phase with a pallid, bluish gray pelt that suggests a partial albinism. Fur graders normally see only a handful of blue lynx among the thousands of pelts handled annually (D. Craig, pers. commun.), and there seems to be no consistent point of origin. However, blue lynx are thought to be more common in northwestern Canada, particularly in the Yukon Territory.

The paws of the lynx are broad, producing a snowshoelike effect that enables the animal to traverse deep snow easily. The "weight load on track," or weight per surface area of the foot, is 34–38 g/cm² (0.48–0.54 pounds/inch²) (Van Zyll de Jong 1963). This is a vital adaptation for the pursuit of the lynx's principal prey, the snowshoe hare (*Lepus americanus*). Bobcats have shorter legs and smaller feet and are less mobile in deep snow. Parker et al. (1983) found that the paw of the lynx supports twice as much weight on snow as that of the bobcat. As a result, mean snow accumulation appears to be the most important factor limiting the northern distribution of the bobcat, and the two species are essentially allopatric. Even where the geographic ranges of lynx and bobcat overlap, their niches are segregated by winter range conditions (McCord and Cardoza 1982). The ability of the bobcat to successfully secure food in deep snow is influenced by topography, forest cover, and snow conditions (i.e., frequent crust formation would provide the bobcat with greater mobility). Such variables make it difficult to identify a critical threshold snow depth above which the bobcat is unable to survive.

The lynx is further distinguished from the bobcat by a lighter, less spotted pelage and longer ear tufts. Whereas the tip of the tail of a bobcat is black only on the upper side, that of a lynx is all black. The black fur on the back of the lower hindlegs of the bobcat contrasts with the lighter beige fur of the lynx.

DISTRIBUTION

The lynx ranges across nearly all of Canada and Alaska (Fig. 1). Lynx are at home in boreal forests and are not well adapted to other habitats. There are periodic reports of dispersal southward into settled areas and north onto the tundra, but these movements are ephemeral and occur because of periodic collapses of snowshoe hare populations in the core range (Banfield 1974, Mech 1980).

Lynx will inhabit farming country, but only if it is interrupted by extensive woodlands. The prehistoric distribution of North American lynx (Fig. 1) is largely intact, although some of the southern range is lost. Lynx are thought to have originally occupied parts of the northern continental United States but then retreated during the 1800s in the face of the settlement of the midwestern United States and southern Canada. The historic loss of lynx range in Europe and Asia has been more serious. Lynx have been extirpated from much of central Europe, although the species is found in the Balkans, Czechoslovakia, and Spain (McCord and Cardoza 1982). Lynx are common in Sweden and less so in Finland and Norway. Lynx range extensively throughout Asia from Iran to the Arctic, but have withdrawn from much of the settled portion of the Soviet Union (McCord and Cardoza 1982).

LIFE HISTORY

Reproduction

The breeding season of the lynx is short, occurring between mid-March and early April. Mating behavior has not been fully described. Females generally breed first as yearlings (during their
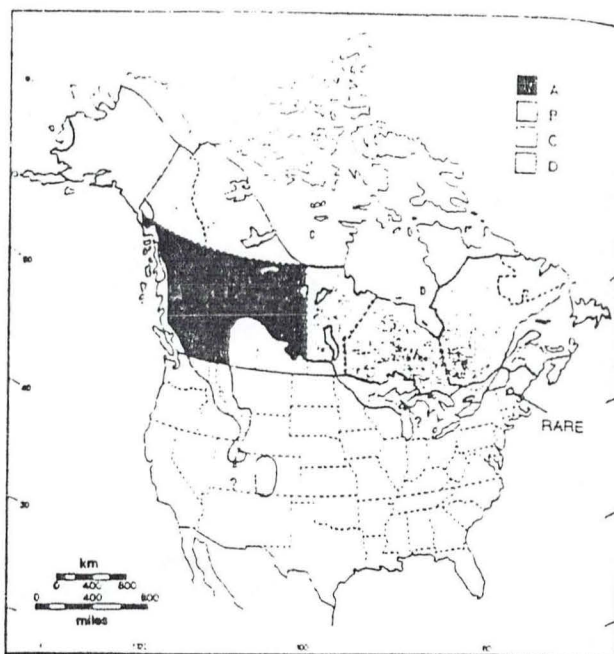

Fig. 1. Distribution and harvest density of the lynx (*Felis lynx*) in Canada and the United States for the 1983–84 trapping and hunting seasons (based on a survey by M. Novak and A. J. Satterthwaite, Ont. Minist. Nat. Resour.). *Legend:* (A) 101–300 km²/animal harvested (area = 1,752,000 km²); (B) 301–1,000 km²/animal (5,493,000 km²); (C) ≥ 1,001 km²/animal (134,000 km²); (D) no harvest (364,000 km²). Total current Canadian and U.S. range is 7,743,000 km². Note that presence is not confirmed in Michigan and Utah. (2.59 km² = 1 mile²)

second winter), but age at onset of sexual maturity is variable (Nava 1970, Brand and Keith 1979). When food is abundant and lynx are in good condition, many females will breed during their first winter (Nava 1970, Brand and Keith 1979; N. Quinn, unpubl. data). Male lynx are thought to be incapable of breeding as kits (Saunders 1961, Stewart 1973).

The gestation period is 9 weeks and young are born during late May and early June. Kits stay with females during their first winter (Saunders 1963, Brand et al. 1976) but probably become less dependent as winter progresses. Family groups break up during late winter at the onset of breeding (Saunders 1963).

Several researchers have used counts of ovarian structures (Fig. 2) and placental scars (Fig. 3) to study reproduction in lynx (Saunders 1961, Van Zyll de Jong 1963, Nava 1970, Stewart 1973, Brand and Keith 1979, Mech 1980, Parker et al. 1983; N. Quinn, unpubl. data). Ovarian structures persist in lynx, however, and corpora lutea of the recent breeding season are difficult to distinguish from corpora albicantia of previous seasons (Nellis et al. 1972, Brand and Keith 1979) (Fig. 2). Accordingly, counts of ovar-
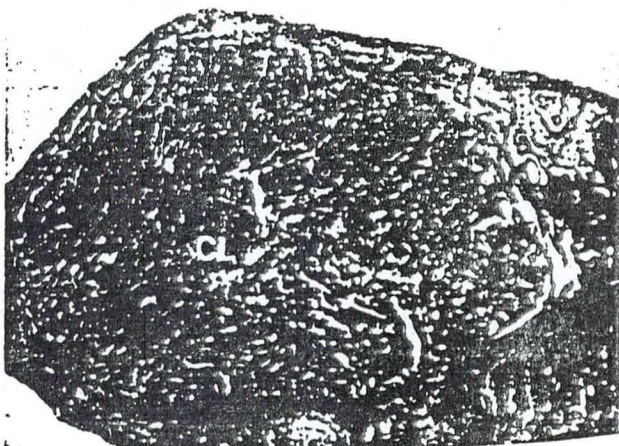

Fig. 2. Cross section of a lynx ovary showing a large corpus luteum (CL) occupying most of the ovary. (Photo. I. Watt.)
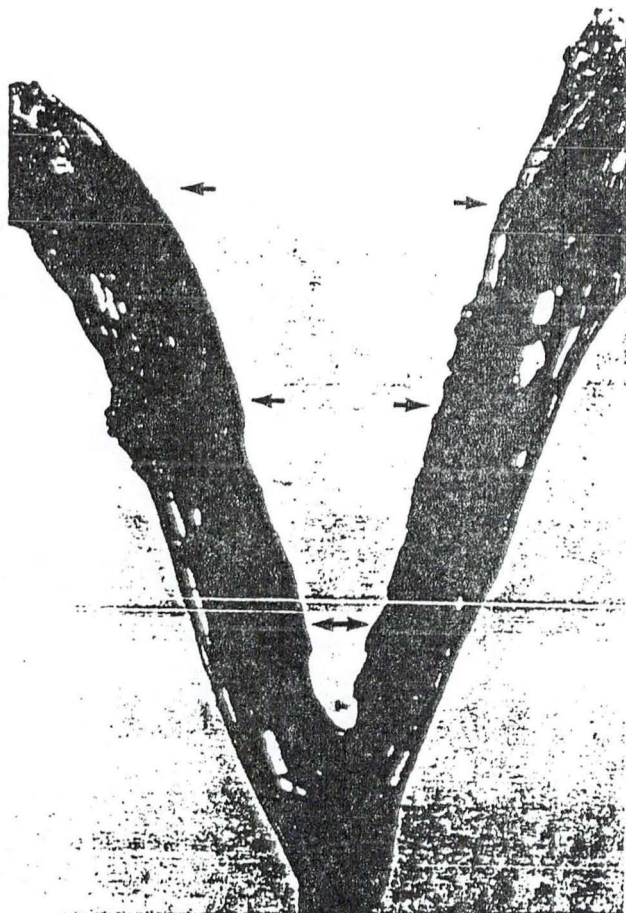
Fig. 3. The uterus from an adult lynx showing darkly pigmented placental scars of embryos from last pregnancy. (Photo: G. Parker.)

ian scars cannot reliably measure the previous season's production of young. Placental scars of lynx are thought to persist postpartum throughout the winter (Nava 1970) but fade between years (Fig. 3); however, these assumptions need further testing. N. Quinn (unpubl. data) observed considerable variation in the faded placental scars of winter-caught lynx from northeastern Ontario and considered that some of the previous year's scars may have faded entirely. Nevertheless, researchers have used counts of placental scars from winter-caught specimens to measure the production of young during the previous spring.

Food availability directly affects the production and survival of young in lynx. The number of young per litter will decline during periods of hare scarcity. For example, in utero sizes of adult lynx in Alberta decreased from a mean of 4.6 to one of 3.4 as hares became scarce (Brand and Keith 1979). Newborn kits weigh about 200 g (7 ounces) (Saunders 1961) and are blind and helpless. Growth and development are also related to food availability. When food is abundant kits grow rapidly; the eyes open at about 14 days and weaning is accomplished by 12 weeks. Kits will weigh about 4.5 kg (10 pounds) by midwinter. When food supplies fail, as happens periodically, growth is retarded; few kits survive and recruitment to the breeding population essentially ceases (Brand and Keith 1979). These periodic failures of recruitment are the immediate cause of lynx population declines (Brand and Keith 1979).

Whether the lynx is an induced or spontaneous ovulator is disputed. The domestic cat (Felis catus) is generally considered to be an induced ovulator and the same has been assumed for lynx. However, Scott and Lloyd-Jacob (1955) observed that the domestic cat can ovulate spontaneously, and Van Zyll de Jong (1963) believed that spontaneous ovulation occurs in lynx. Fritts and Sealander (1978) considered the bobcat to be a spontaneous ovulator. The balance of current opinion is that both the lynx and the bobcat are at least partly spontaneous ovulators.

Mortality

The population cycle of lynx is essentially a predator–prey–forage interaction (Brand and Keith 1979). The dominant mortality factors are probably starvation of kittens and, in recent years, trapping of adults (see Population Dynamics). There is no evidence that other mortality factors such as disease play important roles in the population regulation of lynx. However, malnutrition may predispose lynx to parasites and infections, and disease could play an as yet undefined role.

Little is known about the parasitology of the North American lynx. Studies in Alberta, the Northwest Territories, and Ontario (Van Zyll de Jong 1966a, Smith et al. 1986) have shown that lynx host a diverse parasitic fauna, and most species identified were common to all three areas. Several nematodes were observed, including Toxascaris and Toxocara, the common intestinal worms of domestic dogs (Canis familiaris) and cats, and Troglostrongylus, which can cause pneumonia in zoo animals. Hookworms and several species of tapeworms (Taenia spp.) are also common. A particularly interesting parasite of lynx is the colonial nematode Cylicospirura felineus. These worms inhabit small cysts on the inner wall of the stomach, and there may be as many as 70 worms in each cyst. The cysts probably do not interfere with the normal function of the stomach, and thus the parasite is not considered to be a serious problem for the lynx (Pence et al. 1978). The life cycle of this roundworm is unknown. The lack of helminth species in lynx probably reflects the dominance of one prey (snowshoe hares) in the diet (Smith et al. 1986).

Rabies has been observed in lynx (McCord and Cardoza 1982), although it is considered relatively uncommon. Lynx are also susceptible to panleukopenia (feline distemper) (McCord and Cardoza 1982). The epizootiology of both diseases in lynx populations is unknown.

Lynx have few natural enemies. Gray wolves (Canis lupus) will kill lynx that they catch in the open (Banfield 1974). A record exists of a wolverine (Gulo gulo) killing a trapped lynx (Berrie 1973). The major predator of lynx may be lynx themselves. An attack by an adult (probably a male) on two kits has been reported (Elsey 1954). Infanticide seems common in carnivores and may play a role in the population regulation of some felids (Keith 1974). However, such behavior is not known to be an important factor in the regulation of lynx populations.

FOOD HABITS

Nearly all of the several studies of the food habits of the lynx (Table 2) have shown that lynx feed almost entirely on snowshoe hares (Fig. 4), particularly when hares are abundant. Hares normally constitute at least 60% of the winter diet and about 40% of the summer diet. Other prey include mice (Peromyscus spp.) and voles (Clethrionomys spp. and Microtus spp.), red squirrels (Tamiasciurus hudsonicus), flying squirrels (Glaucomys spp.), ruffed grouse (Bonasa umbellus), and ptarmigan (Lagopus spp.). When hare populations decline, lynx can switch to these other prey (Brand et al. 1976). However, only snowshoe hares can support high density lynx populations (Brand and Keith 1979).

Lynx kill approximately two hares every 3 days. Kill rates vary with the density of hares. Brand et al. (1976) reported that the mean daily consumption rate of adult lynx was 37% greater during winters of hare abundance than during winters of scarcity. Lynx will cache hares but do not always return to the cache site (Nellis and Keith 1968). Lynx will eat vegetation (Saunders 1963), and grass is often found in the stomachs of trapped lynx (Saunders 1963, Stewart 1973). However, such observations are usually interpreted as aberrant feeding behavior after capture. Predation on large mammals is uncommon. Lynx occasionally will kill deer (Odocoileus spp.) and caribou (Rangifer tarandus) fawns and moose (Alces alces) calves (Saunders 1963), and, in rare cases, adult deer or caribou. However, deer or moose hair found in lynx scats is most often obtained through scavenging, and lynx are not considered important predators of ungulates. A notable exception occurs on Newfoundland Island, where lynx prey heavily on caribou calves (Bergerud 1983). Lynx were extremely scarce in Newfoundland and probably preyed on the native arctic hare (Lepus

Table 2. Studies of the food habits of the Canada lynx

Location	Season	% prey items[a]						Source
		Snowshoe hare	Mice and voles	Squirrels	Grouse	Other birds	Other[b]	
Alberta	Winter	35–90	4–28	9–12	2–6	3–6	2–15	Brand and Keith (1979)[c]
Alberta	Winter	69		1	13		17	Nellis and Keith (1968)[d]
Alberta/ Northwest Territ.	Summer	33	19	11	3	19	14	Van Zyll de Jong (1966a)[f]
	Winter	60	7	1	7	10	13	Van Zyll de Jong (1966a)[f]
Newfoundland	Summer	45	21			21	15	Saunders (1963)[e]
Ontario	Fall	63			6	13	19	Stewart (1973)
	Winter	70	4	3	5	5	13	Stewart (1973)
Cape Breton Island	Winter	93	3	1	3			Parker et al. (1983)[g]

[a] Data are from analysis of stomach contents unless otherwise indicated; numbers are the number of occurrences as % of all occurrences for all items unless otherwise indicated.
[b] Primarily carrion, vegetation, and unidentified remains.
[c] Figures vary according to hare density.
[d] Data are from observations of lynx kills.
[e] Numbers are % of total weight.
[f] Converted from % occurrence.
[g] Numbers are % of total volume.

arcticus) prior to the introduction of the snowshoe hare during the 1860s. The introduced snowshoe hare population flourished, as did lynx. When the snowshoe hare population first declined, the lynx (now common) through necessity may have learned to prey on caribou calves. Lynx predation on caribou calves was so heavy that it became the primary factor limiting the growth of the caribou population (Bergerud 1983). Thus a "prey switching" system (Bergerud 1983) developed, and the dynamics of Newfoundland's caribou herd now depends, in part, on the status of the hare population (Bergerud 1983). However, the recent growth of caribou populations on Newfoundland Island has reduced the importance of lynx predation on total calf mortality.

The Eurasian lynx, being larger than the North American lynx (McCord and Cardoza 1982), apparently preys more often on large mammals such as roe deer (Capreolus capreolus). However, hares and small animals remain important components of its diet (Haglund 1966).

BEHAVIOR

Lynx are considered solitary, unsociable animals that associate only during the brief mating season. However, a recent study has suggested that lynx may not be as antisocial as once thought.

Fig. 4. The diet of the lynx consists predominantly of snowshoe hares. (Photo: N. Quinn.)

Researchers on Cape Breton Island found evidence that lynx met regularly in spruce (Picea spp.) bogs, apparently to socialize (Parker 1981). Adult males, nevertheless, are incompatible in captivity. Home ranges overlap, particularly among animals of different ages and sexes (Nellis et al. 1972, Brand et al. 1976), but adult lynx of the same sex seem to be mutually hostile and keep essentially exclusive ranges (Berrie 1973, Mech 1980). Lynx manage to avoid each other across the landscape through scent-marking by urination. Lynx seem preoccupied by this behavior and urinate frequently, as often as 32 times/km (52 times/mile) traveled (Saunders 1963). Bobcats, and possibly lynx, have evolved complex rituals of scent-marking that involve urine, feces, and anal gland secretions (Bailey 1973). This behavior may serve to indicate an individual's age and sex, and may help to maintain the social structure of populations.

Lynx are usually more active at night than during the day. Daily activity patterns, however, appear to be influenced by hunting success. A hungry lynx will usually wander more than a well-fed one. An extreme example is the extensive wanderings by lynx during years of hare scarcity. Felids have a poorly developed sense of smell and rely heavily on vision to detect prey. The eyes of lynx are well adapted for night hunting, having abundant rods in the retina that intensify light and help to discern form. In addition, the eyes are oriented forward on the skull for the stereoscopic vision needed by predators to judge distance from prey.

Lynx exhibit a variety of hunting behaviors. The most common technique is to randomly search good snowshoe hare habitat to flush prey from cover. Success of the ensuing pursuit depends on several factors, including snow depth and hardness and initial distance from prey (Nellis and Keith 1968). The success rate of chases can vary from 9% to 42% (Saunders 1963, Nellis and Keith 1968, Parker et al. 1983). A second technique is simply to lie in wait for hares near concentrations of trails (Brand et al. 1976). Adult females with kittens may hunt cooperatively, especially during winter (Saunders 1963, Barash 1971, Parker et al. 1983). Several lynx will advance on a front through promising habitat and flush and pursue hares together.

ECOLOGY

Habitat

Habitat selection of lynx is not well understood and needs further study. Lynx depend on the snowshoe hare as their principal food and, presumably, good hare habitat is good lynx habitat. There have been several studies of snowshoe hare habitat selection (Bider 1961, Wolff 1980, Orr and Dodds 1982, Wolff et al. 1982, Pietz and Tester 1983). Snowshoe hares prefer diverse forest with alternate stands of swamp conifer for cover and shrubby openings for feeding. In parts of western Canada the aspen (Populus spp.) uplands forest supports high densities of hares and lynx. In most conifer-dominated habitats, dense softwoods in

association with openings of 2–4 ha (5–10 acres) are ideal. Parker (1981) determined that lynx have highly specific habitat requirements. Lynx selected for successional habitats and open mature conifer and against mature mixed-wood forest during winter (i.e., selected for habitats most frequented by hares). Use of conifer habitat increased during summer. Mature deciduous-dominated forests and dense alder (*Alnus* spp.) swales were avoided during both summer and winter (Parker 1981). Any irregular pattern of logging or fire in boreal forest should produce prime hare (and lynx) habitat.

Home Ranges

The home ranges of lynx are normally about 16–20 km² (6–8 miles²) but can vary from 12 to 243 km² (5–94 miles²) (Saunders 1963, Berrie 1973, Brand et al. 1976, Mech 1980, Parker et al. 1983). Home ranges of males are greater than those of females. Brand et al. (1976) did not observe a clear relationship between the home range sizes of lynx and the population densities of lynx and hares. However, their sample was small, and factors such as habitat quality and prey availability likely influenced home range size. Mech (1980) studied a transitory population in Minnesota and observed unusually large home ranges. He speculated that this was due to relaxed social pressures caused by the relatively sparse population. The variation in the spatial organization of lynx populations throughout the cycle is poorly understood and merits study. For example, if lynx concentrate in pockets of hare abundance during population declines, concerted trapping pressure could decimate localized populations.

Population Density

Little information exists on the density of lynx populations, which are extremely difficult to census. Researchers in Alberta studied a population by tracking it for several winters and found that the population fluctuated from almost 0 to 10 lynx/100 km² (39 miles²) (Brand and Keith 1979). Bergerud (1971) used removal trapping to estimate winter densities of 3.9 and 7.7/100 km² in two parts of Newfoundland. Parker et al. (1983) estimated 20 lynx/100 km² on a restricted study area on Cape Breton Island. A summary of estimated lynx densities from various regions of its range is provided in Table 3. It appears that lynx can reach densities as high as 1/5–10 km² (2–4 miles²) during peak numbers in restricted areas of favorable habitat and as low as 1/50–70 km² (19–27 miles²). Most densities appear to fall within the range of 1/15–25 km² (6–10 miles²). Like most carnivores, however, the abundance of lynx will show significant regional variation depending on the availability of favorable habitat and food.

Population Dynamics—The Cycle

Researchers first recognized the synchronous relationship between lynx and snowshoe hare populations decades ago (Elton and Nicholson 1942). Naturalists observed a 10-year cycle in the harvest of hares in the Hudson's Bay Company records from the 1800s and found that the harvest of the lynx followed the same pattern with a short lag. For years this has been considered a textbook example of the relationship between a predator and its prey. Only recently, however, has the mechanism of the hare–lynx cycle been clarified (Brand and Keith 1979).

The basic cause of the cycle is the interaction of the snowshoe hare with its food supply (Keith 1974). Snowshoe hares can reach astounding abundance; densities of 1,700/km² (4,403/mile²) have been recorded (Brand et al. 1976). As hare populations increase, they overbrowse their range and the absolute availability of food becomes limiting. Food quality also declines (Sinclair and Smith 1984). When browsed, certain woody plants such as willows (*Salix* spp.) and alders respond by producing secondary compounds, including terpenes. These compounds inhibit the digestion of protein by certain species of herbivores. Thus, as hares become abundant, they are forced to rely on a dwindling and unpalatable food supply (Bryant 1981, Bryant et al. 1985).

The initial decline in hare numbers is probably due to starva-

Table 3. Estimates of lynx population density from various studies.[a]

Density (km²/lynx)	Lynx population status and location	Source
11.4 and 13.5	Density during two successive highs in a 125-km² area in Alberta	Brand et al. (1976)
49.9	Density during a low in Alberta	Brand et al. (1976)
43.5	Density during an earlier low in Alberta	Brand et al. (1976)
17.9	High population in central Russia	Iurgensen (1955)
58.8	Low population in central Russia	Iurgensen (1955)
13.0–25.6	Density 5 years after hare population peak (low cycle) in Newfoundland. Represents a pocket of abundance during a low.	Bergerud (1971)
4.9	High population on Cape Breton Island	Parker et al. (1983)
7.7–18.1	Moderately high population near Tok, Alaska, early winter 1982–83	Stephenson (1984)
16.6–18.6	Moderate early winter population following peak numbers in good habitat along the Wood River, Alaska. By late winter, numbers had declined to 1/33.9–45.3 km² as a result of trapping that removed 17 lynx, or about 51.5% of the population.	R. Stephenson (unpubl. data)
4.9–10.1	Density during 1973–74 peak, Kenai Peninsula, Alaska	T. Bailey (unpubl. data)
21.8–76.7	Various areas on the Kenai Peninsula, Alaska, during 1977–82	T. Bailey (unpubl. data)

[a] Source: Stephenson (1984).

tion, followed by several years when malnutrition and predation combine to produce high mortality. Predation alone is believed sufficient to depress hare densities during the final period of decline (Keith et al. 1984).

As stated above, lynx strongly depend on snowshoe hares for food. As hare populations decline, lynx cannot find an adequate alternate food resource and their populations "crash." However, the decline is due not so much to starvation as to a sudden drop in the production and survival of young. Female lynx in poor condition will produce smaller litters. As the decline continues, fewer females breed and the survival rate of the few kits produced is extremely low. Recruitment virtually ceases at the low point of the cycle. Brand and Keith (1979) developed a model to illustrate the impact of changing mortality rates on adult and juvenile lynx during different phases of the population cycle in a study area in Alberta (Table 4). Nontrapping mortality of kittens during the population decline approached 100% (Table 5).

The cycle reverses after the respective food resources begin to recover. This predator–prey–forage interaction has established an apparently perpetual cycle of about 10 years (Fig. 5). Such unstable systems are typical of wildlife populations in relatively simple northern ecosystems where the diversity and abundance of resources are limited.

An intriguing aspect of the lynx cycle (and indeed of many boreal wildlife cycles) is that it is roughly synchronous across vast areas. The intensity of the lynx harvest for Ontario and Quebec for the 30-year period 1919–20 through 1950–51 is similar in chronology to that for Alaska, especially for the period 1919–20 through 1930–31 (Fig. 6). A continental spatial pattern of the hare cycle is well established; the cycle initiates and emanates recurringly from central Canada (Smith 1983). Keith (1974) hypothesized that the fluctuations of associated hare popula-

Table 4. Estimates of annual rates of trapping and nontrapping mortality among lynx populations in Alberta during 1964–67 and 1971–75 [a]

Biological year (May–May)	A Lynx per 100 km2 Rochester[b]	B Estimated lynx population in May (before births) A × 531,000 km2	C Finite rate of reproductive increase[c]	D Lynx population in May (after births) B × C	E Total lynx trapped over winter[d]	F Remaining lynx[e]	G Lynx population in following May (before births)[f]	H Nontrapping mortality rate (%) (May–Nov) (F–G)/ D × 100	I Trapping mortality rate (%) (Nov–March ED) (F–G) × 100
1964–65					6,495		45,100		13
1965–66	8.5	45,100	(1.5)[g]	67,650	1,638	66,012	20,200	68	8
1966–67	3.8	20,200	(1.5)[g]	30,300	1,098	29,202	12,200	56	8
1971–72					22,776		53,100		30
1972–73	10.0	53,100	2.4	127,440	18,084	109,356	40,900	54	31
1973–74	7.7	40,900	1.8	73,620	8,056	65,564	20,200	62	29
1974–75	3.8	20,200	1.5	30,300	3,445	26,855	16,500	34	17

[a] Source: Brand and Keith (1979).
[b] Data from Brand et al. (1976).
[c] See Brand and Keith (1979) for calculations of reproductive increase.
[d] Data from Obbard et al. (1987) and A. W. Todd (pers. commun.).
[e] The theoretical number of lynx present in May if all mortality was due to trapping.
[f] Column B of subsequent row.
[g] Reproductive increase for 1965 and 1966 was assumed similar to that observed during 1974, as hare population levels were similar.

Table 5. Estimates of nontrapping (May–Nov) mortality rates among kittens and adult lynx in Alberta, 1972–74. [a]

Year	A N kittens born in May[b]	B N adults present in May[c]	C N kittens present in November[d]	D N adults present in November[e]	Kitten mortality (%) (May–Nov) (A – C)/A	Adult mortality (%) (May–Nov) (B – D)/B
1972	74,340	53,100	26,000	33,000	65	38
1973	32,720	40,900	1,700	26,600	95	35
1974	10,100	20,200	1,200	18,700	88	7

[a] Source: Brand and Keith (1979).
[b] Calculated from Table 4 as B × (C – 1).
[c] Table 4 column B.
[d] Calculated as percent kittens times fall population estimate, D – (F – G); see Table 4.
[e] Calculated as percent adults times fall population estimates, D – (F – G); see Table 4.

tions tend to get out of phase but are periodically synchronized by continent-wide mild winters. Clearly, the Canadian harvest of lynx could not exhibit a definite cycle if populations were not more or less in phase across the country.

Due to the spatial synchrony of the lynx cycle, evidence that lynx are declining in one area is probably applicable across broad regions. This hypothesis warrants further testing.

MANAGEMENT
Sexing and Aging Techniques

The lynx, similar to other felids, can be readily identified to sex by examination of the genitalia. Although males are generally heavier and larger than females of the same age, body size cannot

be confidently used as a means of differentiating between sexes. The inability to confidently identify lynx to sex by criteria other than genitalia makes it impossible to assign sex to lynx observed in the wild or in traps.

The age of lynx can be determined from dentition and cementum annuli deposition. Kits (young of the year) acquire their permanent teeth during their first winter, and kits can be distinguished from adults by examining the basal foramen of the canine teeth, which normally remains open until their second winter (Saunders 1961). However, a study of bobcats in Kansas
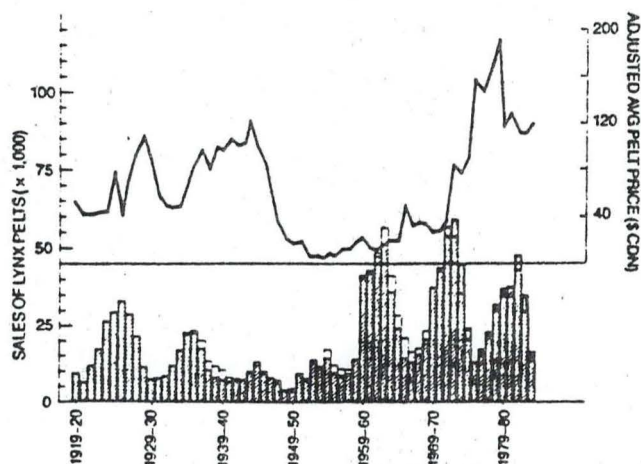
Fig. 5. Sales of lynx pelts in Canada (hatched bars) and the United States (pre-1970, open bars; post-1970, stippled bars). Solid line shows adjusted average price (1970 $CDN = 1.0) Source: Obbard et al. (1987).
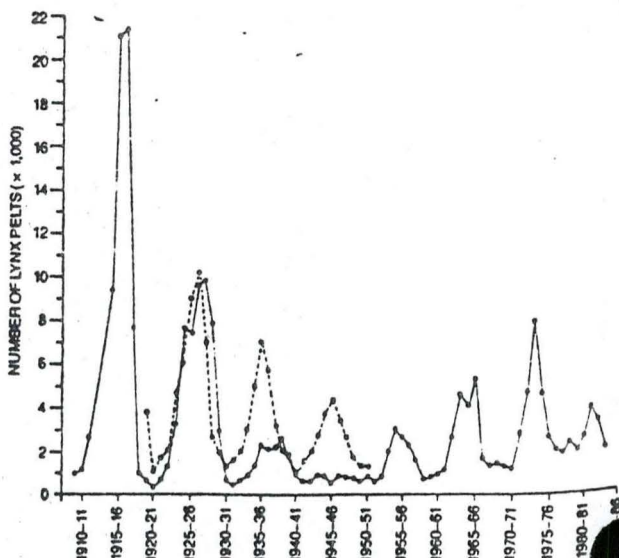
Fig. 6. The cyclical nature of lynx harvests as shown by the number of lynx pelts exported from Alaska (solid line) from 1909–10 through 1983–84 (Stephenson 1984) and the number of lynx pelts harvested in Ontario and Quebec (broken line) from 1919–20 through 1950–51 (Obbard et al. 1987).

ranginanus). This expansion of range is probably the result of ameliorating weather and habitat alterations having created more favorable habitat for small mammals and deer. Evidence suggests that lynx densities will decline with ingression of the bobcat. Managers should be aware of this factor when appraising regional situations and interpreting regional hare–lynx cyclical patterns.

In eastern Canada the sporadic distribution of lynx, which is probably a response to the expanding range of the bobcat, means that different management approaches are required. In New Brunswick, where the lynx is uncommon (especially in the southern part of the province), the species has never been trapped. In Nova Scotia, where the lynx is found only on the highlands of Cape Breton Island, harvests are regulated on a quota basis and lynx can be trapped only during years of abundance. Lynx were formerly abundant on Newfoundland Island, where, when hares were scarce, lynx preyed on caribou calves. Because this was considered a serious problem during the 1960s, lynx were systematically removed from certain caribou calving grounds. However, lynx densities have recently declined and restricting the annual harvest has been considered. Increases in pelt value and trapping pressure may also lead to reduced densities.

On the Kenai National Wildlife Refuge in Alaska (Bailey et al. 1986), wildlife managers have concluded that excessive trapping was the major contributing factor to the recent depression in lynx densities, despite increases in snowshoe hares. They recommended that the season be closed during periods of hare scarcity in highly accessible areas and that a quota system, similar to that on Cape Breton Island, be used when lynx densities increase. Their recommendations represented a practical and reasonable approach designed to ensure maximum cyclical resiliency by the lynx population and optimum economic benefit to the user. It is a management plan that benefits from the availability of the required data mentioned earlier, and it should represent a "model" for lynx management in other regions of North America.

There is every reason to be optimistic about the future of the Canada lynx and the continued contribution of the species to the fur trade in North America. The challenge to the furbearer manager is to assess the regional status of the lynx, snowshoe hare, and bobcat, evaluate trapping pressure, analyze those factors relative to our present knowledge of their interrelationships, and develop a management plan that will ensure optimum use of a viable lynx population.

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(Photo: J. Milette)

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(Photo: M. Elderkin)

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animals or cavity nesters a reader tube is available that can be inserted into the burrow or cavity and that will read the transponder number each time the animal enters or leaves. The data may be automatically recorded by a computer wired to the reader. A newer version of the Handwand/Reader is powered by an internal battery that makes it convenient for field use.

The failure rate of the transponders tested in this study was 30%. Tests by Identification Devices, Inc. engineers indicated that the polypropylene casing allowed minute amounts of moisture to enter and short-circuit contacts. Identification Devices, Inc. has recently developed a glass casing that does not allow leakage and should eliminate most failures. We are currently testing these in the laboratory in 14 black-tailed prairie dogs (*Cynomys ludovicianus*), and they have been in place for 20 weeks with no failures.

Domestic ferrets have thick skin for a small animal. It was difficult to penetrate their skin with the needles originally provided with the implanter unit or with 12-gauge needles purchased from other sources. Therefore, it was necessary to sharpen needles prior to each use. Identification Devices, Inc. is currently working on the development of a disposable syringe and needle.

DYNAMICS OF AN EXPLOITED CANADA LYNX POPULATION IN ONTARIO

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Abstract: Population structure, mortality, productivity, and condition of lynx (*Felis lynx*) from zones of distinctly different harvest density and forest type in northeastern Ontario were contrasted. These population parameters were remarkably consistent and showed little variation across the 107,000-km² study area. Productivity was high; 33% of kits and nearly all yearling and adult females bred, and mean litter size was 4.18. The mean rate of trapping mortality over several years was 46 ± 26% for males, 28 ± 17% for females, and 38% overall. Trapping accounted for nearly all mortality experienced by the population. The population increased in face of this rate of harvest. Trapping mortality appeared uniform across the study area. The data suggest that population density of lynx is lower in boreal coniferous forest than in boreal mixed-wood forest.

The Canada lynx is a commercially important furbearer that is harvested across most of its range. However, the biological basis of lynx population management is deficient. Lynx are practically impossible to census and management strategies are often based solely on trends of the harvest. The mean value of lynx pelts has increased to >$500.00 (Can.) and there is concern that such high prices may result in overexploitation.

The impact of commercial trapping on lynx populations is not fully understood. In Ontario furbearer harvests are regulated via quotas on legally delineated traplines. Determination of allowable harvests of some species, including lynx, is left essentially to the judgement of local wildlife officers. There are areas of the province in which the harvest of lynx is consistently higher than others yet reasons for this are unclear. Spatial variation of the harvest could be due to some intrinsic quality of the populations, such as productivity, or simply to the discretion of local managers. We contrasted the structure, mortality, condition, and productivity of lynx populations from zones of distinctly different harvest density (harvest/unit area) and forest

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type. Our objectives were to determine mechanisms of response of lynx populations to trapping and identify factors, both intrinsic and extrinsic to the population, which might account for the wide geographic variation of the harvest of lynx in Ontario.

We wish to thank the many trappers, biologists, and conservation officers who contributed. J. F. Gardner provided the inspiration for the study and D. Barnacal, P. D. Gray, and E. M. Addison were particularly helpful. D. G. Joachim, I. D. Watt, and C. L. Levangie assisted in aging specimens. D. Fraser gave freely of his time to do the calculations for trapping mortality estimates.

METHODS

Collection and Laboratory Procedure

Lynx carcasses were collected from trappers in a 107,000-km² area of 8 Ontario Ministry of Natural Resources administrative districts in northeastern Ontario (Fig. 1) during 3 trapping seasons (25 Oct–28 Feb 1979–82). Carcasses were identified according to date and location of capture.

We classed lynx as kits during the 1st winter of life and yearlings during their 2nd winter. Lynx older than yearlings were classed as adults. Kits were identified by incomplete closure of the basal foramen of canines (Saunders 1963). Age of older specimens was determined by counting cementum annuli (Johnson and Watt 1980, Kvam 1984).

Productivity was assessed by analysis of reproductive tracts of females. We sectioned ovaries with a hand-held tool and tried to count luteal bodies under low magnification. However, as noted by Brand and Keith (1979), the luteal bodies could not be reliably segregated, and we ultimately recorded only whether a specimen had ovulated or not. Placental scars were counted by 1st soaking the uteri overnight in water to clear coagulated blood. The uterine horns were then separated, split longitudinally, and spread on a white dissecting pan under bright light. Scars were counted without magnification. We considered counts of placental scars to be in utero litter counts but recognize that some scars were probably sites of fetal mortality. Placental scars were evaluated only for the 1980–81 and 1981–82 seasons.

Physical condition was indexed by weighing renal fat (all fat associated with kidneys, ureters, and bladder) to the nearest 0.1 gram.

Mail Survey

A mail survey was used to provide an index to snowshoe hare (*Lepus americanus*) population density from which the status of lynx populations was inferred (Brand and Keith 1979). During mid-winter in each year of the study, trappers throughout the study area were asked: (1) Do you think snowshoe hare are; (a) abundant, (b) average, or (c) scarce on your trapline this year?, and (2) Have hare populations; (a) increased, (b) decreased, or (c) not changed this year?

Harvest Density Zones

From maps of distribution of the harvest, we identified 3 zones (Fig. 1) that had very different harvest density during 1978–81. The period beginning in 1978 was selected because lynx populations began increasing throughout the collection area in 1978–79 (see Results). Zone 1, termed "low," was 70,127 km² and had a mean annual harvest of 0.34 lynx/100 km² during 1978–81. Zone 2, termed "medium," was 31,158 km² and had a mean annual harvest of 0.70 lynx/100 km². Zone 3, termed "high," was 5,314 km² and mean annual harvest was 1.71 lynx/100 km². We contrasted the structure, mortality, physical condition, and productivity of lynx populations from these 3 zones.

Forest Regions

Canada's forested land has been delineated into regions and "sections," based on flora and physiography (Rowe 1972). Our study area falls within the Northern Clay (NC), Central Plateau (CP), and Missinaibi Cabonga (MC) sections of the Boreal Forest Region and the Temagami (T) section of the Great Lakes St. Lawrence Forest Region (Fig. 1). The forests of the MC and T sections are very different in composition and structure from the NC and CP forests. The MC and T sections are diverse, mixed forest on varied topography and soils, whereas the NC and CP are true boreal forest, having vast stretches of nearly monotypic coniferous forest on flat plains.

We thus established 2 forest "regions" for purposes of this study; the "Boreal Mixed Wood" (MC and T sections) and the "True Boreal" (NC and CP sections). The Boreal Mixed Wood Region had relatively more forest in early succession from logging, burn, or insect damage than the True Boreal (27 vs. 17%, respectively)
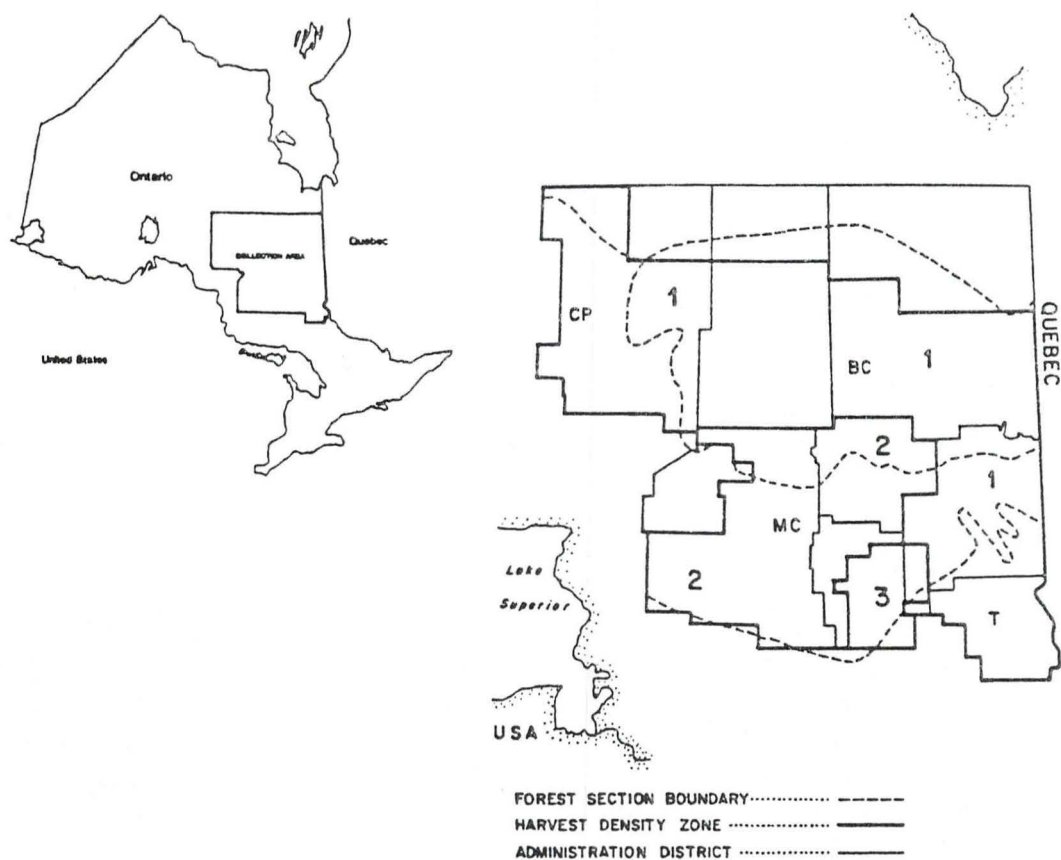
Fig. 1. Lynx carcass collection area, northeastern Ontario, 1979–82, showing harvest zones and forest regions.

and average clearcut size was smaller (160 vs. 560 ha) (J. Kekanovich, pers. commun.).

Analysis of Mortality

Total mortality was estimated by life table analysis in a manner similar to that of Rolley (1985) for bobcats (*Felis rufus*). The instantaneous rate of increase of the population ($\bar{r}$, Caughley 1977) was estimated from the rate of change of annual harvest (thus using the harvest as an index of population density) and used to produce a "corrected" life table (Rolley 1985). Age distributions were combined among years to approximate a representative sample (Rolley 1985). Brand and Keith (1979:839) suggested that increasing lynx populations have more or less constant rates of age-specific recruitment and mortality and thus rapidly develop a stable age distribution.

Trapping mortality was estimated by the Fraser-Paloheimo (F-P) statistic (Paloheimo and Fraser 1981, Fraser 1984). These authors showed

that for populations undergoing sex-selective harvest, the rate of change of sex ratio with age is determined by harvest mortality rate. They provided a non-linear least squares model (the F-P statistic) to estimate harvest rate of each sex based on this relationship. A close approximation of the model, which estimated overall (sexes combined) harvest mortality, can be achieved by weighted linear regression of percent males on age (Fraser et al. 1982). Harvest mortality is estimated by the inverse of the age at which the proportion of males decline to 50%. Male lynx are more vulnerable to trapping than females (Van Zyll de Jong 1963, Berrie 1971, Stewart 1973, Bailey et al. 1986, this study), and thus, the F-P statistic may be applicable to lynx.

The technique requires several conditions. First, nonharvest mortality and dispersal must have little effect on sex ratio. No sex-selective natural mortality factor of lynx has been reported, and the bias of dispersal is minimal for large study areas such as ours (Fraser et al. 1982).
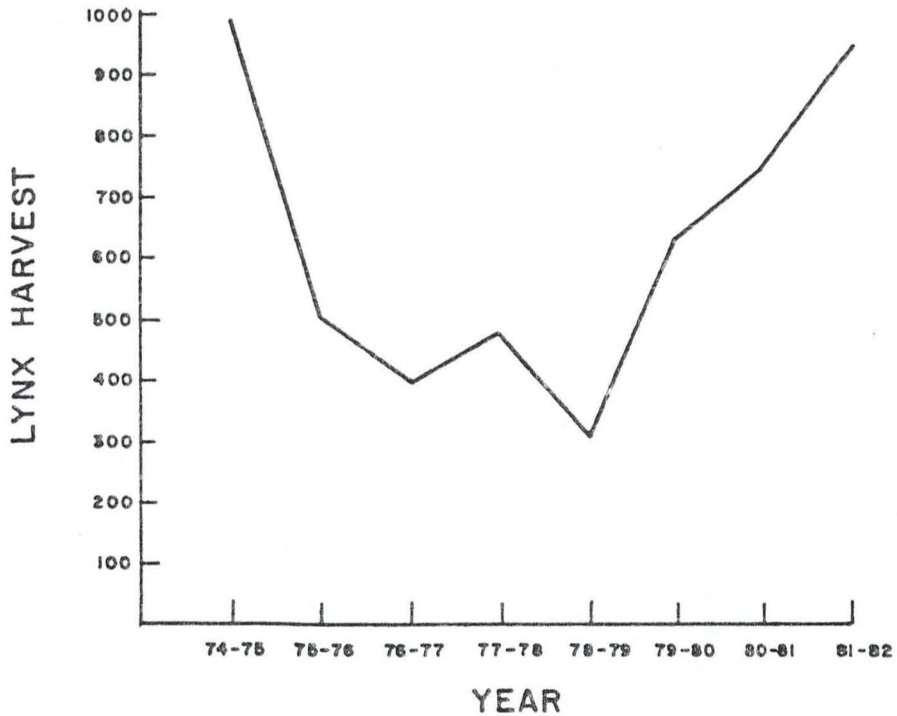
Fig. 2.   Lynx harvest in northeastern Ontario collection area, 1974–82.

Second, trapping effort must be either constant or measured during the period that animals in the sample are subject to harvest. There was no measure of trapping effort available for this study, but despite a rapid increase in the value of lynx pelts in the late 1970's, there is reason to believe that trapping effort was more or less constant. The period of open season and number of trappers in the collection area did not change during the period represented by the sample. In addition, under a registered trapline system where the harvest is essentially dictated by set quotas, trapping effort may be independent of pelt value. Further, trapping of "land fur" has, in large part, been non-selective; traps are often set to catch any of several species. Thus, effort expended on lynx has been determined, in part, by the overall effort on land fur which local managers feel has been more or less constant in recent years. A 3rd condition of the model is equal sex ratio at recruitment, and the age of onset of sex-differential mortality must be known. Kits are recruited at an even sex ratio, and male vulnerability begins at 1.5 years of age (see Results). In short, the F-P statistic seems to be applicable to this data set and perhaps to lynx populations elsewhere.

Comparative statistical analyses were by Chi-square, analysis of variance (ANOVA), and Mann Whitney and t-tests. Unless otherwise indicated, statistical significance was considered at $P = 0.05$.

Table 1.   Age and sex distribution of lynx trapped in the northeastern Ontario study area, 1979–82.

Age	Sex			Total
	♂	♀	Unknown	
Kit	92	88	8	188
1	298	186	4	488
2	91	79	2	172
3	24	16		40
4	3	15		18
5	5	5		10
6		3		3
7	1	4	1	6
8		2		2
9		2		
10				
11				
12				
13		1		1
Unknown[a]	44	19		63
Total	558	420	15	993

[a] Could not be aged due to lab error, etc. None of these were kits.

Table 2. Age and sex distributions of lynx in northeastern Ontario, 1979–82, by harvest density zone and forest region.

| | Harvest zone[a] | | | | | | Forest region[b] | | | |
| | Low | | Medium | | High | | Boreal Mixed Wood | | True Boreal | |
Age	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
Kit	50	53	25	23	12	11	42	37	49	37
1	174	108	78	55	31	18	147	93	117	75
2	52	43	24	29	11	5	39	34	44	35
3	15	9	5	4	3	2	8	7	13	7
4	2	5	1	7		3		10	2	5
5	1	3	2	1	2	1	5	2		1
6				1		2		3		
7				1		2		3	1	
8										
9		2								2
13				1				1		
Totals	294	223	135	122	59	44	241	190	226	162

[a] Low = 0.34, medium = 0.70, and high = 1.71/100 km².
[b] See text for explanation.

RESULTS

Mail Survey

Results of the mail survey were remarkably consistent across the collection area; 419 responses were received and abundant or average (Question 1) and increasing or not changed (Question 2) were the favored responses in all 8 administrative districts each year. In no case did the response for scarce or decreased exceed 15%. Observation by field staff supported these data. We concluded that hare populations were at or near cyclic high density throughout the study area.

The lynx harvest in the collection area peaked in the mid-1970's, reached a low in 1977–78 (2 districts) or 1978–79 (6 districts), and increased since that time (Fig. 2). We concluded from these harvest statistics, the hare survey, and productivity data to be presented, that lynx populations were increasing throughout the collection area during the study.

Harvest Structure

Nine hundred ninety-three specimens were collected; 319 in 1979–80, 343 in 1980–81, and 331 in 1981–82. The overall age and sex distribution (Table 1) shows 3 notable features: (1) abundance of yearlings followed by a sudden decline of numbers with age; (2) dominance of males from ages 1 to 3, resulting in an overall sex ratio favoring males; and (3) relative scarcity of kits.

The adult-yearling sex ratio, 58♂:42♀ (Table 1), was significantly different from 50:50 (χ^2 =

Table 3. Composite life table for lynx in northeastern Ontario, 1979–82. Harvested lynx were assumed to be a sample of the dying and were entered in the d_x column.[a] (Life table was corrected for the observed rate of increase [$r = 0.331$].)

| | | | | | Correction factor e^{rx} (B) | Corrected | | |
Age[b]	Sampled frequency	d_x	l_x (A)	s_x		d_x	l_x (A × B)	s_x
0.5		434	1,175[b]	0.630	1.179	168	1,385	0.879
1.5	488	488	741	0.341	1.643	638	1,217	0.476
2.5	172	172	253	0.320	2.288	321	579	0.446
3.5	40	40	81	0.506	3.187	76	258	0.705
4.5	18	18	41	0.561	4.439	40	182	0.780
5.5	10	10	23	0.565	6.182	30	142	0.789
6.5	3	3	13	0.769	8.609		112	
7.5	6	6	10	0.400	11.989	53	120	0.558
8.5	2	2	4	0.500	16.697	20	67	0.701
9.5	2	2	2	0.000	23.252	47	47	0.000

[a] The l_x column represents the no. of animals alive at the beginning of each age interval and s_x is the proportion surviving from age N_T to N_{T+1}.
[b] No. of age-0.5 lynx estimated from age specific reproductive rates and an estimate of kit survival to fall (see text).

Table 4. Mean placental scar counts (of specimens with scars) of lynx from 3 harvest density zones, and 2 forest regions, northeastern Ontario, 1979–82.

| | Harvest zones[a] | | | | | | | | | Forest regions[b] | | | | | |
| | Low | | | Medium | | | High | | | Mixed Boreal | | | True Boreal | | |
Age	Scars	N	$\bar{x}$ with scars	Scars	N	$\bar{x}$ with scars	Scars	N	$\bar{x}$ with scars	Scars	N	$\bar{x}$ with scars	Scars	N	$\bar{x}$ with scars
1	4.37	71	27	3.33	21	43	2.00	9	33	3.38	43	30	4.38	50	32%
2	4.43	25	84	4.33	16	75	3.00	2	100	4.00	21	81	4.69	21	76%
3+	4.73	11	100	4.43	7	100	4.50	6	66	4.46	15	87	4.67	5	100%

[a] Low = 0.30, medium = 0.70, and high = 1.71/100 km².
[b] See text for explanation.

22.50, df = 1, $P < 0.01$). Such differential harvest of males could produce highly skewed adult sex ratios in very heavily exploited populations. To investigate this, we contrasted adult sex ratios among harvest density zones. Data were combined among years because of limited samples. Adult sex ratios of the harvest density zones were: Zone 1 (low) 53:47, Zone 2 (medium) 43:57, and Zone 3 (high) 52:48 (Table 2). These ratios were not significantly different ($\chi^2 = 2.11$, df = 2, $P > 0.10$). Adult sex ratios also were not significantly different in the Boreal Mixed Wood (46:54) and True Boreal (55:45) forest regions ($\chi^2 = 1.47$, df = 1, $P > 0.10$).

Mortality

The composite life table computations are arrayed in Table 3. The sampled age distribution was entered in the dx column and thus treated as a sample of the dying. Yearlings greatly outnumbered kits in the age-sex distribution compiled over 3 years (Table 1), and thus, kits were underrepresented in the harvest. Kits were entered in the life table as an estimate calculated from age specific rates of productivity (Table 4) and a literature-based estimate of survival. Brand and Keith (1979) estimated annual survival of kits in an increasing lynx population to vary from 40 to 80%. We assumed 80% survival to the trapping season but recognize that the value is arbitrary. The instantaneous rate of increase, calculated from the trend in harvest of 1978–81 (Fig. 2), was 0.33 (Table 3).

Total annual mortality rate for each age class can be calculated directly from Table 3 by subtracting the Sx column (survival) from 1.0. Mortality from age 0.5–1.5 was 0.120 and for age 1.5–2.5 was 0.524. Adult mortality was variable but relatively low, being <0.300 in most cases.

Annual rate of trapping mortality over the entire study area was 0.46 ± 0.26 for males and

0.28 ± 0.17 for females (90% CL). The regression approximation of the F-P model estimated the overall (sexes combined) rate of trapping mortality as 0.38, which is well within the range of the sex-specific rates calculated from the more powerful iterative technique. Data were combined among years for both analyses due to inadequate within-year samples. The wide confidence intervals are due to the small number of degrees of freedom, a problem inherent in a population of animals that largely disappears after 4 or 5 years of age (D. Fraser, pers. commun.). (Note that the overall rate of trapping mortality was comparable to or even greater than the age-specific rates of total mortality [Table 3].)

Annual rate of trapping mortality for Zone 1 was 0.40 ± 0.21 for males and 0.25 ± 0.13 for females (90% CL). Unfortunately, data for Zones 2 and 3 and the forest regions were inadequate for application of the F-P technique (D. Fraser, pers. commun.). However, trapping mortality rate of Zone 1 was only slightly different than that of the entire study area and the age at change of sex ratio was 3 or 4 in all cases (Table 2). Thus, the data suggest that the rate of trapping mortality was not very different across the study area.

Condition

Mean renal fat weight of male and female kits was similar (13.13 g, [$N = 84$] for males and 12.45 g [$N = 80$] for females, $P > 0.10$). Males had significantly more renal fat in the yearling (38.37 g, $N = 284$ vs. 27.59 g, $N = 171$), 2-year-old (45.83 g, $N = 76$ vs. 30.71 g, $N = 62$), and ≥3-year-old (65.74 g, $N = 27$ vs. 39.43 g, $N = 36$) age class (Students t-test, $P < 0.05$ in all cases). Renal fat also tended to increase with age (Table 5). These results are biased by differences in size among age and sex classes (Quinn and Gardner 1984). However, the rel-

ative magnitude of differences in renal fat weight exceed those of body size (Quinn and Gardner 1984); therefore, these data probably reflect real differences in condition. There were no significant among-year differences in renal fat for any age-sex class (ANOVA, $P > 0.10$ in all cases).

Renal fat was not conclusively related to forest region or harvest density. Although renal fat weight was higher in the True Boreal Forest than the Boreal Mixed Wood Forest for 6 of 8 age-sex classes (Table 5), only weights of female kits were significantly different. Similarly, although renal fat weight was highest in the "low" density trapping zone in 5 of 8 age-sex classes, only weights of male kits and yearlings were significantly different among harvest density zones (Table 5).

Productivity

The occurrence of luteal bodies was high; 96% of 157 yearlings, 99% of 69 2-year olds, and 100% of 43 females ≥ 3 years of age had ovulated. Lynx begin breeding in March (McCord and Cordoza 1982), and all specimens of this study were caught before March. Therefore, the yearlings must have ovulated during previous seasons as kits.

The majority of lynx aged 2 and 3+ had placental scars (80%, $N = 45$ and 92%, $N = 27$, respectively). However, only 33% of yearlings ($N = 103$) had placental scars. Therefore, although nearly all kits had ovulated (above), only 1 in 3 were impregnated. The mean of placental scar counts for females with scars was 3.88 for yearlings ($N = 34$), 4.30 for 2-year olds ($N = 36$), 4.40 for ≥ 3-year olds ($N = 25$), and 4.18 overall. There was no significant difference between years (81 vs. 82) in placental scar counts for any age class (Mann Whitney U-test).

Productivity was compared across harvest density zones and forest regions (Table 4) by testing both percent females pregnant and the distribution of placental scar counts of impregnated females for 3 age classes. Sample size from the high harvest density zone was considered inadequate for certain of these tests (Table 4). Percent females pregnant was not significantly different in any case. Although placental scar counts tended to decrease with harvest density and were consistently higher in the True Boreal Forest (Table 4), only counts of yearlings between forest regions were significantly different (Mann Whitney U-test). We conclude that pro-

Table 5. Mean renal fat weight (g) of lynx from 3 harvest density zones, and 2 forest regions, northeastern Ontario, 1979–82. Means followed by the same letter are significantly different (ANOVA or Student's t-test, $P < 0.05$).

				Harvest zones[a]							Forest regions[b]					
	Low		Medium			High			Boreal Mixed Wood			True Boreal				
Age	♂	N	♀	N	♂	N	♀	N	♂	N	♀	N	♂	N	♀	N
Kit	12.75 A	47	14.49	47	8.50 A	22	8.54	21	21.85 A	13	10.84	9	15.73	36	7.93 C	34	11.00	42	14.25 C	35
1	41.74 B	163	26.47	99	32.05 B	75	23.38	47	36.24 B	31	30.86	18	36.14	139	28.84	84	41.93	109	27.83	68
2	46.91	48	32.83	37	40.23	22	20.64	26	59.79	9	24.28	5	42.80	35	27.87	31	48.41	41	32.50	32
3+	73.50	17	45.01	19	56.15	6	20.76	13	47.15	4	34.38	9	59.38	12	36.30	24	70.83	15	39.17	14

[a] Low = 0.34, medium = 0.70, and high = 1.71/100 km².
[b] See text for explanation.

ductivity was not clearly related to harvest density or forest region.

DISCUSSION

The principal descriptive features of this population have been observed in several other harvested lynx populations (Saunders 1961, Van Zyll de Jong 1963, Berrie 1971, Stewart 1973, Brand and Keith 1979). The apparent age- and sex-related vulnerabilities to trapping have been attributed to differences in behavior among age-sex classes. The vulnerability of yearling males, for example, has been attributed to high mobility (Saunders 1963, Van Zyll de Jong 1963, Mech 1980) and probably accounted for the high overall mortality of yearlings observed here.

Population parameters of lynx were remarkably uniform across the vast geographic area of this study. Variation in productivity, for example, could not be clearly attributed to ecological differences between forest regions. There also was evidence that rate of trapping mortality was similar across the study area. If so, lynx populations were sparser in the more northerly forests where harvest density was lower. The carrying capacity for lynx of the Boreal Mixed Wood forests may indeed be relatively high. Habitat selection of lynx has not been fully described, but Parker et al. (1983) reported that lynx prefer a diverse forest environment and selected successional habitat in both winter and summer. The Boreal Mixed Wood forests of this study area provided a more heterogeneous and disturbed (logged or burned) environment than the True Boreal forests and were, presumably, better lynx habitat. Nevertheless, renal fat was higher (albeit not significantly) in the True Boreal forests suggesting that quality of habitat of the coniferous wetlands was at least comparable. Perhaps our classification of forests was too broad to measure quality of lynx habitat. Although the overall carrying capacity for lynx of the Boreal Mixed Wood forests may be higher than the True Boreal, lynx may find prime habitat in disturbed sites in both regions. Local wildlife managers believe that distribution of lynx in the coniferous forests is "spotty"; i.e., lynx are relatively sparse but have loci of abundance.

Lynx populations decline because of high post-natal mortality, and declining populations will have essentially no kits in the harvest (Brand and Keith 1979). Brand and Keith believed that declining lynx populations are vulnerable to overharvest and proposed that trapping be curtailed during population declines. This management strategy is confounded by the high rate of incidental capture of lynx, particularly in red fox (*Vulpes vulpes*) sets. Selective trapping techniques must be developed and promoted to facilitate species-specific management. One option in this regard is live release. Lynx are extraordinarily docile in traps and some trappers in northern Ontario release unwanted animals routinely.

Determining optimum levels of harvest of increasing lynx populations also is a difficult problem. This population increased despite annual trapping mortality of approximately 40%. Yet trapping mortality is additive to natural mortality of lynx (Brand and Keith 1979), and if trapping can be the dominant mortality factor, as reported here, there may be a level of trapping effort that will slow or even reverse the population recovery. Bailey et al. (1986) documented an apparent overexploitation of lynx in Alaska. Trapping mortality ranged from 44 to 86% and also accounted for virtually all mortality in that population. There is pressing need for research to establish guidelines for appropriate levels of harvest of lynx and certain other boreal furbearers across the broad range of habitats.

There is nothing in the F-P technique that precludes use in fluctuating populations (D. Fraser, pers. commun.) and the technique may have broader application to lynx as it may in black bear (*Ursus americanus*) (Fraser et al. 1982). We caution, however, that our trapping mortality estimates are biased if there is a sex-related natural mortality factor of lynx. Male lynx disperse farther and are more mobile than females (Saunders 1963, Bailey et al. 1980, Mech 1980), which could very well result in higher natural mortality of males.

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Felis lynx Linnaeus, 1758

Lynx

Felis lynx Linnaeus, 1758:43. Type locality near Upsala, Sweden.
Lynx vulgaris Kerr, 1792:157. Type locality Sweden (=*Felis lynx* Linnaeus).
Lynx canadensis Kerr, 1792:157. Type locality eastern Canada (=Quebec).
F(elis) borealis Thunberg, 1798:14. Type locality forests of northern Sweden.
Felis kattlo Schrank, 1798:52. Type locality Bohemia.
Felis lyncula Nilsson, 1820:14. Type locality Scandinavian forests.
Felis cervaria Temminck, 1824:106. Type locality Asia.
Felis pardina Temminck, 1824:116. Type locality Lisbon, Portugal.
Felis lupulinus Thunberg, 1825:189. Type locality North Scandinavia.
Felis vulpinus Thunberg, 1825:192. Type locality Uppsala, Sweden.
Felis virgata Nilsson, 1829:pls. 3-4. Type locality Sweden.
Felis isabellina Blyth, 1847:1178. Type locality Tibet.
Lynx cervaria Fitzinger, 1870:108. Type locality Norway.
Lynx subsolanus Bangs, 1897:49. Type locality Codroy, Newfoundland.
Lynx pardella Miller, 1907:398. Type locality Coto Doñana, Huelva, Spain (new name for *pardina* Temminck thought to have been preoccupied by *Lynx pardina* Oken).
Lynx sardiniae Mola, 1908:48. Type locality Nuoro, Sardinia.

CONTEXT AND CONTENT. Order Carnivora, Family Felidae, Subfamily Felinae, Genus *Felis*, Subgenus *Lynx*. *Lynx* is here recognized as a subgenus in compliance with taxonomic arguments by Van Gelder (1977), although Kratochvil (1975) believed subfamilial classification (Lyncinae) might be justified. The number of genera, species, and subspecies is much debated. Matjuschkin (1978) and Werdelin (1981) suggested that *lynx*, *canadensis*, and *pardina* are specifically distinct under the generic designation *Lynx*. The context and content used herein is not definitive, but is a conservative view of lynx taxonomy, treating these forms as subspecies. The subgenus *Lynx*, then, includes two extant species: *F. lynx* and *F. rufus*. At least eight subspecies are recognized (Corbet, 1978):

F. l. canadensis (Kerr, 1792:157), see above (*mollipilosus* Stone is a synonym).
F. l. isabellina Blyth, 1847:1178, see above (*tibetanus* Gray, *kamensis* Satunin, and *wardi* Lydekker are synonyms).
F. l. kozlovi (Fetisov, 1950:21). Type locality Barun-Burinkhan, Salenginskiy region, Buryatskaya ASSR, USSR.
F. l. lynx Linnaeus, 1758:43, see above (*vulgaris* Kerr, *borealis* Thunberg, *kattlo* Schrank, *lyncula* Nilsson, *cervaria* Temminck, *lupulinus* Thunberg, *vulpinus* Thunberg, *virgata* Nilsson, *orientalis* Satunin, *dinniki* Satunin, *wrangeli* Ognev, *alba* Kerr, *melinus* Kerr, *baicalensis* Dybowski, and *guttata* Smirnov are synonyms).
F. l. pardina Temminck, 1824:116, see above (*pardella* Miller is a synonym).
F. l. sardiniae (Mola, 1908:48), see above.
F. l. stroganovi Heptner, 1969:1260. Type locality Glazkovka, Supunskiy reserve, Primorsk territory, Lake Baikal, USSR (new name for *Lynx lynx neglectus* Stroganov, preoccupied by *Felis neglecta* Gray).
F. l. subsolanus (Bangs, 1897:49), see above.

DIAGNOSIS. Lynxes are distinguished from other *Felis* by the slender nasal branch of the premaxilla, the thinner, less depressed, and sharper postorbital processes, shallower notching of the suborbital edge of the palate, and proximity to the canine and

more forward setting of P3 (Pocock, 1917a). In the Nearctic, *F. lynx* differs from *F. rufus* in the following: black tip completely encircles tail; anterior condyloid foramen (hypoglossal canal) distinct from posterior lacerate (jugular) foramen; presphenoid wider (>6 mm); upper carnassial longer (>16.6 mm); interorbital breadth greater (>30 mm); smaller postorbital processes; and tail shorter than one-half length of hind foot (Durrant, 1952; Hall, 1981; Merriam and Stock, 1932). Palearctic *F. lynx* can be distinguished from the caracal (*Felis caracal*) by the former having spots on the fur and a facial ruff (Werdelin, 1981), and distinction of the anterior condyloid from the posterior lacerate foramen (Van den Brink, 1970). *F. l. pardina*, however, also has confluence of these foramina in common with the caracal, but differs from the caracal (and *F. l. lynx*) in having no metaconid on m1 (Van den Brink, 1970). The presphenoid is wide in *F. lynx* but narrow in *F. caracal* (Ognev, 1935; Van den Brink, 1970).

GENERAL CHARACTERS. Prime winter pelage consists of long, thick fur that is yellowish gray to grizzled grayish brown; summer pelage is shorter, more ragged, pale, and brownish (Durrant, 1952; Jackson, 1961; Saunders, 1961). Lynx fur is spotted to varying degree, depending on the subspecies. The ears are brown with a central silvery-gray spot, and terminate in long (approximately 4-5 cm) black ear tufts (Ognev, 1935). The eyelids, chin, inside of ears, underparts, and throat are white. A flared facial ruff, short tail, and short body with long legs are characteristic (Fig. 1). Digitigrade posture is supported by large, spreading, well-furred paws possessing five toes on the forepaw and four on the hind (McCord and Cardoza, 1982). The digits are joined by a web (No-
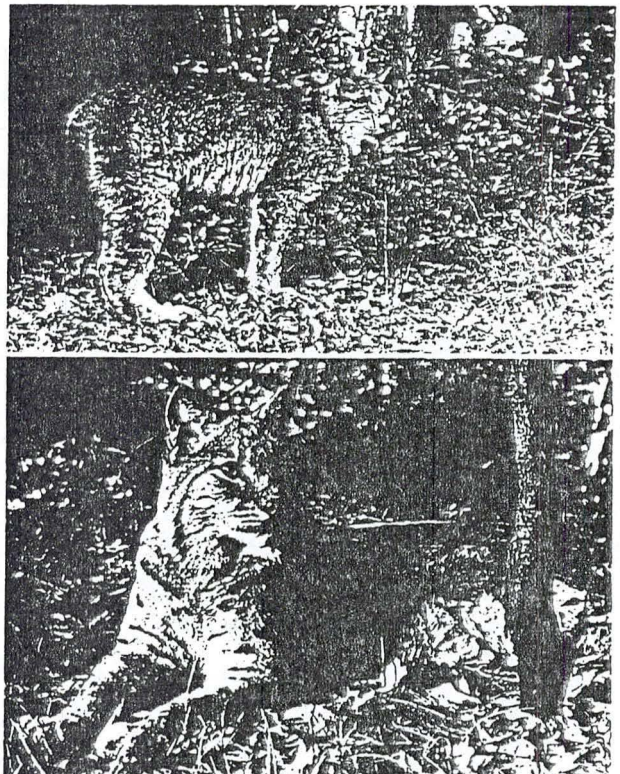

FIG. 1. Photograph of Canada lynx, *F. l. canadensis* (upper), by Tom J. Ulrich, and of European lynx, *F. l. lynx* (lower) from the Carpathian Mountains of Czechoslovakia by Josef Stehlík.

and Alaska (Nava, 1970), respectively, as follows: total length, 825 to 954, 910 to 1,545, 820 to 1,050 (sans tail), 740 to 1,070, 780 to 1,050, 670 to 850; tail length, 95 to 125, 110 to 245, 200 to 310, 50 to 130, 80 to 120, 70 to 130; length of hind foot, 203 to 250, no data, no data, 190 to 260, 210 to 250, 180 to 250.

The permanent dental formula for *F. lynx* is i 3/3, c 1/1, p 2/2, m 1/1, total 28; for deciduous dentition, i 3/3, c 1/1, p 2/2, m 0/0, total 24 (Saunders, 1961, 1964). The skull of *F. l. canadensis* (Fig. 2) was described by Durrant (1952) as being large with small postorbital processes on the frontals, and having a transversely wide presphenoid constricted anteroposteriorly. The posterior palatine foramina are situated near the orbital rim of the palate, the anterior margin of the interpterygoid fossa is semicircular, and the anterior condyloid foramen is separate from the posterior lacerate foramen. The rostrum is abbreviated. Hall (1981) provided skull measurements (in mm) for North American lynx as follows: greatest length, 120 to 136; zygomatic breadth, 82 to 93; alveolar length of maxillary toothrow, 38.1 to 41.6. Cranial measurements for *F. l. lynx* include: greatest length, 131 to 153; zygomatic breadth, 91 to 106.2; length of upper tooth row, 45.7 to 51.9 (Ognev, 1935).

DISTRIBUTION. The lynx has a Holarctic distribution (Fig. 3). Primary habitats in the Nearctic include boreal forests with openings, rugged outcrops, bogs, and thickets (Berrie, 1973; Koehler et al., 1979; Nellis, 1971; Saunders, 1961). Palearctic habitats include old-growth taiga, mixed or deciduous forests, and wooded steppe up to an elevation of 2,500 m (Iurgenson, 1955; Kratochvil, 1968a; Novikov, 1956; Ognev, 1935).

In North America, the range (Fig. 3) of *F. l. canadensis* includes Labrador, Quebec to central British Columbia and the Yukon, Alaska (with the exception of the panhandle and Seward Peninsula) to tree line, northern New England, portions of the Lake States, the Pacific Northwest, and the Rocky Mountains south to Utah, but *F. l. subsolanus* is restricted to Newfoundland (Hall, 1981; McCord and Cardoza, 1982).

Distribution of Palearctic *F. lynx* has changed appreciably during the last 2,000 years largely because of hunting and changes in land use (Eiberle, 1972; Kratochvil, 1968b; Matheson, 1948; Pulliainen, 1964; Van den Brink, 1970). The range (Fig. 3) includes the entire taiga forest from Scandinavia to eastern Siberia, the Iberian peninsula, the Balkan peninsula (Miric, 1974), the Carpathians, Caucasus, and Asia minor, south to Iran and the Kurdish Mountains of northern Iraq, and east through the Siberian forest to the island of Sakhalin, including Mongolia, Manchuria, Chinese Turkestan, the Kopet Dhag of Turkmenistan, southeastern Tibet, the Gilgit, Ladak, and Kashmir regions of northern India, Korea, northern China, and Kamchatka (Corbet, 1978; Ellerman and Morrison-Scott, 1966; Guggisberg, 1975; Matjuschkin, 1978; Novikov, 1956; Ognev, 1935).

Lynx distribution in northern Norway has remained about the same but expansion has occurred in southern Norway (Heggberget and Myrberget, 1980). Lynxes occur regularly between 61°N and 68°N in Norway and Sweden but the most northern distribution is unclear and much debated (Curry-Lindahl, 1969; Mazak, 1968, 1970). In France, lynxes were thought to be nearly extinct until some were found in the Pyrenees (Beaufort, 1965, 1968), and reintroductions have been attempted (Fernex, 1977). Reintroductions also were attempted with some success in Yugoslovia (Cop 1977a, 1977b). Schauenberg (1969) believed lynxes were extinct in Switzerland and Italy. The southern boundary of the range in the western USSR crosses the Moscow, Ryazan, and Vladimir districts (Sysoyev, 1966). In Siberia, the southern limit of the constant range is in pine-birch forests but migrating individuals often travel further south (Azarov, 1976). Mitchell and Derksen (1976) recorded a specimen from Nepal, about 75 km south of the range reported by Ellerman and Morrison-Scott (1966). Hell (1972) believed that the lynx had become extinct in western Europe except in Spain, but since 1950 an increase in the populations of the Carpathian Mountains had occurred. In a symposium on lynx distribution in Europe, populations of lynxes in Norway, Sweden, Finland, Poland, Czeckoslovakia, Rumania, and Yugoslavia were reported to be stable or increasing largely because of reduced hunting, immigration from areas of higher density, and increased food supply (Kratochvil, 1968a).

FOSSIL RECORD. The assumed common ancestor of lynxes, *F. issiodorensis*, is believed to have originated in Africa in the
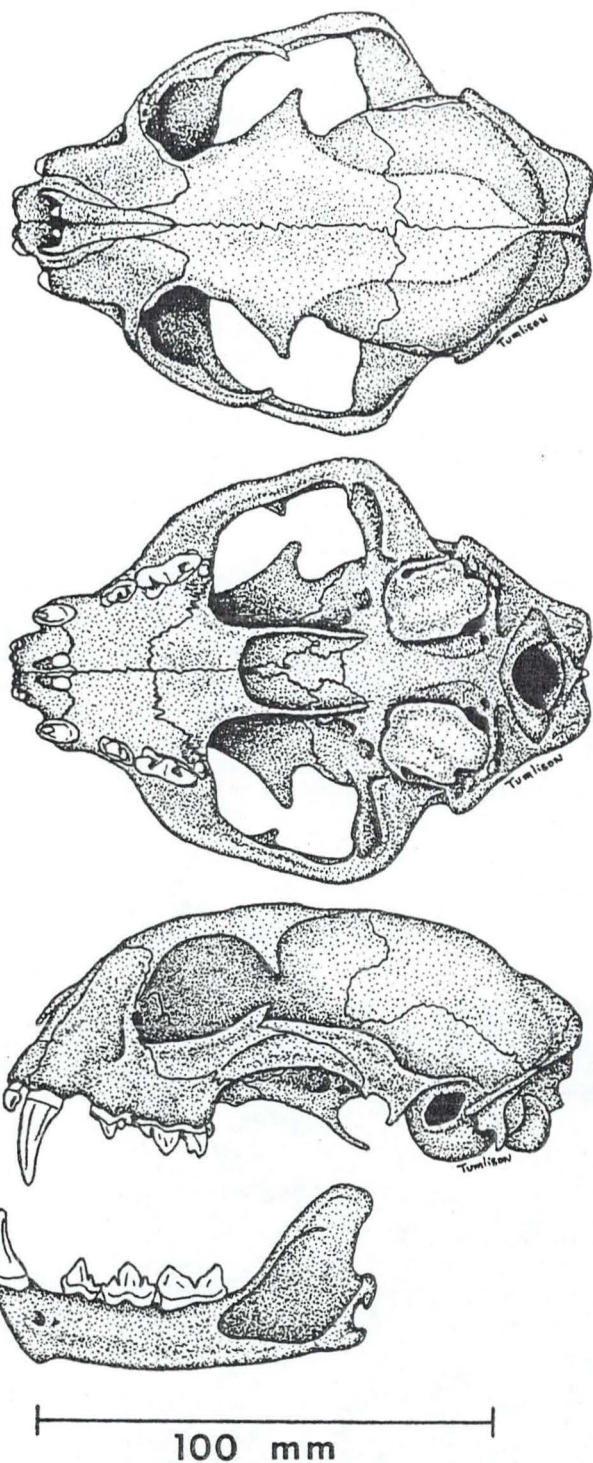

FIG. 2. Dorsal, ventral, and lateral views of skull and lateral view of mandible of *Felis lynx canadensis*. Uncataloged specimen from British Columbia, Canada, housed in the Arkansas State University Museum of Zoology (ASUMZ).

vikov, 1956). Claws are sharp and retractile. The eyes are prominent with ovoid pupils (Nawa, 1967).

The lynx is the largest of the bob-tailed cats, although bobcats are sometimes larger than Nearctic lynxes. Body masses of Nearctic lynxes range from 4.5 to 17.3 kg (Nava, 1970; Saunders, 1961, 1964). Palearctic lynxes are much larger, averaging 17.9 kg for males in Sweden (Haglund, 1966), and reaching 32.0 kg (Ognev, 1935). Kazlauskas and Matuzevicius (1970) reported an old female at 38 kg. Males are generally larger than females. Ranges of standard measurements (in mm) of lynxes from North America (Hall, 1981), northern Europe (Guggisberg, 1975), Russia (Novikov, 1956), Newfoundland (Saunders, 1964), Alberta (van Zyll de Jong, 1975),
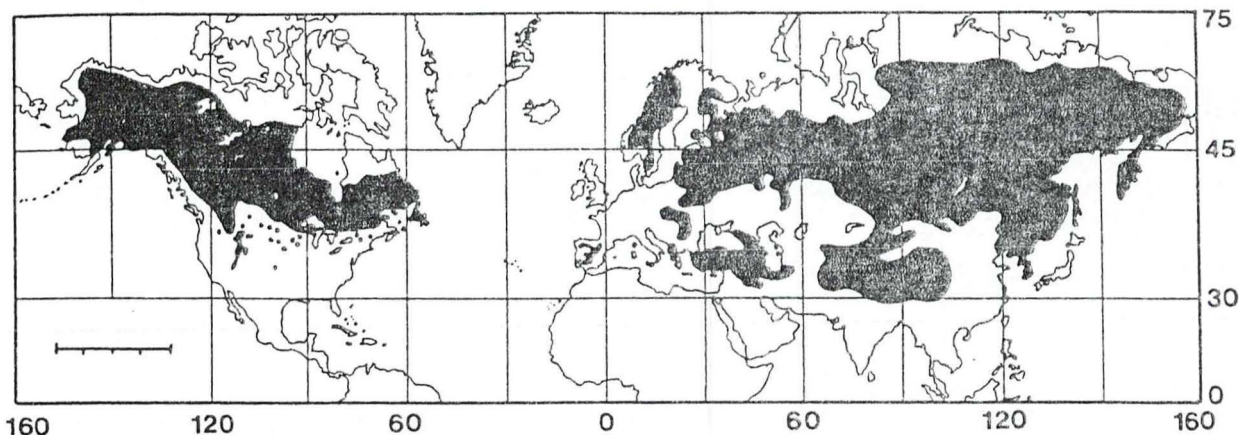
FIG. 3. Distribution of the lynx (*Felis lynx*). Nearctic range modified from McCord and Cardoza (1982) and Palearctic range modified from Matjuschkin (1978). Scale bar equals 4,000 km at the equator.

early to middle Pliocene. This ancestor had lynx-like dental features but skeletally resembled other *Felis*. It is believed to have migrated throughout the northern hemisphere by the middle Villafranchian. *Felis lynx* developed in China and reached Europe from Asia during the Steinheimian land-mammal age of the Pleistocene. It also migrated into North America and gave rise to the Canada lynx (Werdelin, 1981).

Fossil remains of *F. lynx* in North America are recorded from Sangamonian faunas and from the Wisconsinan of Alaska, Idaho, Wyoming, and the Yukon (Kurtén and Anderson, 1980). Records are more common in Europe, including specimens from the F-Emian in the travertines near Weimar and records from the 4-Würm of Italy and the Balkans (Kurtén, 1968a). Specimens are known from the Ipswichian and Devensian of England, the Weichselian of northern Europe, and the Postglacial of England and Denmark (Werdelin, 1981). Fossil specimens have been reported from England (Matheson, 1948), France (Boule and de Villeneuve, 1927), Spain (Sos, 1932), and Greece (Symeonidis et al., 1977).

FORM. Moore et al. (1974) provided detailed descriptions of three forms of guard hair from *F. l. canadensis*. Maximum length of the coarsest hair was 61 mm, maximum diameter 118 µm. The basal medulla is continuous and vacuolated, usually more than one-half the shaft width. Melanin is usually confined to the distal tip and a midshaft band; pigment intensity varies with season and ontogeny (Saunders, 1961).

The hyoid apparatus is held near the base of the skull and is not imbedded in the throat musculature (Pocock, 1916a), therefore the lynx can purr but not roar. In *F. l. isabellina*, the tympanic bulla has a large partition that does not reach the summit of the bulla but terminates toward the inner angle of its anterior edge (Pocock, 1916b). The outer chamber extends more forward than the inner chamber. *F. l. canadensis* differs in that the partition does not advance so far in front so that the anterior part of the inner chamber is broader.

Some external characters of *F. lynx* differ from other lynxes (Pocock, 1917b). The ears are angular, pointed, and tipped with long hairs. The upper margin of the rhinarium is more convex than in other lynxes and the nostrils are somewhat larger, possibly an adaptation to life at higher altitudes. The interramal tuft of tactile vibrissae is absent but the mystacial and superciliary tufts are well developed. Genal tufts are obscured by the long facial ruff, and may consist of a single bristle. The feet of *F. l. isabellina* differ from *F. rufus* by having larger inner lobes of the sheaths of the claws and the plantar pads are shorter compared with their width. The plantar pads are also more overgrown with hair in *F. lynx*.

The distal end of the baculum of *F. lynx* is conical to slightly compressed laterally and slightly decurved (Kratochvil, 1975). The proximal end is bifurcated and the rami are concave on the inner surface. Dimensions (in mm) of the largest os penis were: length, 9.4; greatest width, 3.8; least width, 0.5.

The deciduous carnassial pair is formed by dP3/dp4, but the adult pair is composed of P4/m1 (Saunders, 1961). Greatest sectorial development on dP3 and P4 is seen in the paracones and metastyles that shear along the paraconids and protoconids, respectively, of dp4 and m1. The dP4 and M1 are small and molariform,

but m1 has practically lost the entire talonid. However, Kurtén (1963) suggested an evolutionary return of the metaconid-talonid complex of m1 and the possible return of m2. Supernumerary teeth have been reported (Kratochvil, 1965; Miric, 1973; Vereshchagin, 1959). Manville (1959) reported a bregmatic fontanelle bone in only one lynx cranium (0.002%) from the Yukon territory of Canada, although bobcats possessed these bones in about 15% of the crania examined.

FUNCTION. Under experimental conditions, lynx guard hair had the lowest transmittance of solar radiation among Arctic mammals (Øritsland and Ronald, 1978), indicating that solar heating does not contribute significantly to energy conservation in the species. Thick fur and large, well-furred paws are thermoregulatory and structural adaptations to the Arctic environment (McCord and Cardoza, 1982). Lynxes maintain thermoneutrality but do not change respiratory frequency or minute volume (lung ventilation) at low temperatures, as do other Arctic mammals whose higher winter metabolic rates require greater oxygen consumption. Maximum minute volume is realized at 20°C with a respiratory frequency of 30/min (Casey et al., 1979).

Yearling lynxes have less bone-marrow fat than adults, suggesting greater energetic needs and undeveloped hunting skills (Stewart, 1973). Prey abundance affected renal and subcutaneous fat levels; also renal levels were affected by age, and subcutaneous fat by sex (Brand and Keith, 1979).

Scapino (1981) found that a stiffened mandibular symphysis functions to transfer muscle force from the balancing side of the head to teeth in the working jaw. Claw retraction is a function of the dorsal elastic ligaments but co-contraction of both forearm flexor and extensor muscles is necessary for claw protrusion (Gonyea and Ashworth, 1975). A comparative study of the appendicular skeleton of the caracal and lynx (Mandal and Talukder, 1975) indicated that lynxes had a longer presacral but shorter postsacral ilium and an elongated tibia, and concluded this modification was related to their springing behavior. Auditory, visual, tactile, and taste senses are highly developed, but olfaction is poor (Lindemann, 1955; Saunders, 1963a). Vision in the lynx is predominantly scotopic and is especially suited for perception of fine differences in brightness (Rager and Festetics, 1982).

ONTOGENY AND REPRODUCTION. The breeding season of lynxes varies geographically. In Newfoundland, mating occurred between early March and early April, peaking about the third week of March (Saunders, 1961); in Alaska, from March through April (Nava, 1970); in Alberta in April and May (Nellis et al., 1972). Lynxes in the Palearctic breed in February and March (Haglund, 1966; Novikov, 1956), and as early as January in southern Spain (Guggisberg, 1975). Saunders (1961) estimated that 10% of the ova were lost before implantation, and at least another 13% were lost between implantation and capture. In Alberta, Brand and Keith (1979) found that 73% of adult females conceived in years of snowshoe hare (*Lepus americanus*) abundance, but only 33% when hares were scarce. Gestation period for wild lynxes was estimated at 63 to 70 days (Saunders, 1961) and 67 to 74 days (Matjuschkin, 1978); Haglund (1966) determined a gestation period

of 63 to 73 days for captive European lynxes. Parturition occurs in late May to early June in Newfoundland (Saunders, 1961), and late May in Russia (Matjuschkin, 1978).

Litter sizes in lynxes may range from one to six, but are usually three to four in North America (Brand and Keith, 1979; Nava, 1970; Saunders, 1961) and two to three in the Old World (Novikov, 1956). Younger females tend to have smaller litters (Brand and Keith, 1979). Commonly, there is one litter per breeding season; however, individuals in some populations may have litters only in alternate years (Ognev, 1935; Saunders, 1961).

Newborn lynxes have closed eyes, folded ears, no teeth, poorly developed ear tufts, and well-developed pelage with dark longitudinal streaking on the back and limbs but less dark on the flanks (Merriam, 1886; Saunders, 1964). Lengths and body masses of two neonates in Newfoundland were 163 and 158 mm, and 197 and 211 g (Saunders, 1964). Guggisberg (1975) reported an average body mass of neonates as 70 g, but Stehlík (1983a) reported an average of 289 g (range 250 to 360).

Eyes open between 10 and 17 days after birth (Kunc, 1970; Lindemann, 1955; Novikov, 1956; Wayre, 1969). Young lynxes begin to walk at 24 to 30 days (Lindemann, 1955; Stehlík, 1983a). The pelage of a 2-month old kitten had lost the natal pattern on the body, but the bars on the inner side of the forelegs were more distinct than in newborns. All lacteal teeth had erupted. Lacteal canines possessed an accessory cusp located immediately above the incisors (Saunders, 1961). Eruption of lacteal teeth begins with the canines at about 17 days of age, then continues with the incisors at about 20 days, then premolars at about 30 days (Lindemann, 1955; Stehlík, 1983a; van Zyll de Jong, 1963). Lacteal dentition begins replacement at about 4 months of age (Lindemann, 1955; Saunders, 1961). Young European lynxes reportedly possess dP2 which is not replaced in the adult (Lindemann, 1955), however, van Zyll de Jong (1963) noted that this observation may represent misidentification of dP3 and dP4 as dP2 and dP3. Two-month-old lynxes in Europe had fully developed the ability to groom their body surface (Lindemann, 1955).

The stretch reflex begins at 10 days of age with stretching of the hind legs while lying on the back (Stehlík, 1975). This stretch is accomplished while standing at 14 days, and stretching of the forepaws occurs at 15 days. Stretching of the back appears by the 34th day, and simultaneous stretching of opposite fore and hind limbs is seen at 35 days. Yawning begins at 10 days. Reaction to optic stimuli was observed at 15 to 20 days and to acoustic stimuli at 18 to 20 days (Stehlík, 1983a).

The temporal ridges of the parietals are lyre-shaped but the lyre width decreases with age and joins in later life to form the sagittal crest on the interparietal bone (Saunders, 1964). The lambdoidal ridge also becomes more prominent with age. Epiphyses of long bones of the forelimb remain unossified up to 9 months of age (van Zyll de Jong, 1963). The distal epiphysis of the humerus and proximal epiphysis of the radius are ossified by 18 months, the proximal epiphysis of the ulna is ossified by 21 months, the distal epiphyses of the radius and ulna are ossified by 30 months, and complete ossification of all epiphyses probably occurs at about 32 months (van Zyll de Jong, 1963).

The duration of the suckling period is over 6 months (Lindemann, 1955) but young take meat from 30 days of age (Guggisberg, 1975). At about 40 days, young begin playful motions of stalking prey (Guggisberg, 1975). During ontogeny, litter mates lose their need for kinship and become more "envious" of prey caught by litter mates (Lindemann, 1955).

The litter remains with the mother until the next mating season, and young of late litters have not attained adult size at this time (Lindemann, 1955; Novikov, 1956). Ognev (1935) emphasized that some litters may remain with their mothers after 1 year, which may mean that some lynxes reproduce only in alternate years.

Female lynxes can breed during their first reproductive season, that is, at about 10 months of age (Nava, 1970) but may not breed until 22–23 months (Saunders, 1961; van Zyll de Jong, 1963). Sexual maturity may be delayed during periods of prey scarcity (Brand and Keith, 1979; Nava, 1970) and overall breeding declines during such periods. Parker et al. (1983) reported that reduced prey affected reproductive success in yearling females more than in older females.

Luteal bodies are large and persistent, and increase in number with age (Brand and Keith, 1979; Nellis et al., 1972). Largest Graafian follicles appeared in early March as blister-like prominences on the ovary (Saunders, 1961). Testicular size also increases with age (Nava, 1970). Males apparently do not breed until their second year (Saunders, 1961; Stewart, 1973); gametogenesis may decline during summer and fall (Saunders, 1961; van Zyll de Jong, 1963).

Lynxes have lived almost 22 years in captivity (James, 1977) but seldom surpass 15 years in the wild (Nava, 1970). The primary mortality factors seem to be prey scarcity (Brand et al., 1976; Nava, 1970), that affects kittens and yearlings most, and man (de Vos and Matel, 1952; Mech, 1980).

ECOLOGY. Population irruptions or habitat disruptions sometimes force dispersal of lynxes (Gunderson, 1978; Mech, 1980). Reported long-range dispersal distances for lynxes have increased from 165 km (Nellis and Whetmore, 1969) to 483 km (Mech, 1977). Average daily cruising distance ranges from 5.0 km (Saunders, 1963a) to 19.2 km (Haglund, 1966). Differences in cruising distance are thought to be related to hunting conditions.

Home ranges in lynxes differ by sex, age, prey density, and survey method, from approximately 11 to 50 km² (Berrie, 1973; Brand et al., 1976; Novikov, 1956; Saunders, 1963a). However, a colonizing population of lynxes in Minnesota had home ranges of 51 to 243 km² (Mech, 1980) and lynxes in Riding Mountain National Park, Manitoba, had ranges of 118 to 221 km² (Carbyn and Patriquin, 1983). Larger home-range size could be related to low density of lynxes or low prey density, although Brand et al. (1976) found that lynx home ranges were unrelated to either. Females usually have smaller home ranges than males, and home ranges sometimes overlap (Brand et al., 1976; Mech, 1980; Nellis et al., 1972).

The major food of Nearctic lynxes is snowshoe hares, accounting for as much as 83% (frequency of occurrence) of the diet (More, 1976; Nellis et al., 1972; Saunders, 1963b; van Zyll de Jong, 1966a). These studies also indicate utilization of squirrels (Tamiasciurus hudsonicus, Spermophilus sp.), small mammals (Muridae), beaver (Castor canadensis), deer (Odocoileus sp.), moose (Alces alces), muskrats (Ondatra zibethica), and birds (Galliformes and Anseriformes); some is taken as carrion. Strong selection for hares (Lepus sp.) is believed to have resulted in predator-prey cycles. Brand et al. (1976) found that lynxes responded functionally and numerically to hare density. Palearctic lynxes also rely heavily on lagomorphs, as much as 79% by frequency of occurrence (Aymerich, 1982; Delibes, 1980; Guggisberg, 1975; Novikov, 1956) but cervids are sometimes the major food (Birkeland and Myrberget, 1980; Novikov, 1956). Additional foods in the Palearctic include small mammals (mostly Muridae), squirrels, insectivores, birds (Anseriformes, Galliformes, Passeriformes), reptiles (Squamata), and fish. Seasonal variation in foods is related directly to availability. In Spain (Delibes, 1980), rabbits (Oryctolagus cuniculus) were used most from July through October, ducks (Anas sp.) from March to June, and cervids (Cervus elaphus, Dama dama) from November to January. Nellis et al. (1972) estimated daily food requirements for adult lynxes at 600 g/day. Consumption rates were estimated at 591 g/day (Delibes, 1980) and 960 g/day (Brand et al., 1976); rates vary according to prey abundance (Brand et al., 1976). Hunting success improves with practice and group size (Parker et al., 1983), and has been estimated at 26% in Nova Scotia (Parker et al., 1983) and 36% in Alberta (Brand et al., 1976).

Two hundred years of trapping records from the Hudson Bay Company have shown cyclic fluctuations in F. l. canadensis harvests. These records show a regular periodicity of about 9.6 years but an irregular amplitude of oscillations of trapped lynxes (Elton and Nicholson, 1942). Elton and Nicholson (1942) believed lynx cycles to be geographically synchronous, but more recent investigation indicates that peak collection is first reached in the central provinces, and the western and eastern regions peak later and with less amplitude (Bulmer, 1974; Butler, 1953).

Several attempts have been made to analyze the lynx data by use of autoregressive models. Moran (1953a) used logarithms of the numbers trapped, Bulmer (1974) included a strictly periodic term, Campbell and Walker (1977) used a pure sine wave, and Tong (1977) and Bhansali (1979) considered harmonic components. These statistical treatments are attempts to explain the cyclic fluctuation in lynx populations in mathematical terms, which can aid in prediction of population status.

Sunspot and lynx cycles are not correlated (Moran, 1949), but lynx trapping is correlated with temperature and precipitation (Arditi, 1979; Fox, 1978; Moran, 1953b). Moran (1953b) suggested that the effect of weather on snowshoe hares was responsible

for synchronization of hare-lynx cycles through predator-prey interaction. Fox (1978) believed that forest fires caused plant succession favoring hares, that snowfall accounted for the variation not accounted for by fire, and that oscillation was forced through these events. Arditi (1979) found that a few linear combinations of 3 or 4 months of temperature and precipitation variables fit the lynx population index, with the critical variable occurring between summer and winter.

By use of a predator-prey model, Gilpin (1973) found that hares must "prey" on lynx. He interpreted this to mean that hare abundance could indirectly kill lynx by vectoring a disease, but also suggested that man, by trapping more heavily for lynxes during hare abundance, might artificially cause the lynx oscillation. Weinstein (1977) commented that trapping records may reflect short-term changes in hunting strategy related to hare abundance. Finerty (1979) noted that the phenomenon might be an artifact created by comparing data that are not comparable. Gilpin's (1973) data apparently compared harvests of hares in eastern Canada to that of lynxes in western Canada.

Van Zyll de Jong (1966b) summarized the known occurrence of ectoparasites of lynx, including eight species of fleas. Most fleas encountered were found commonly on rodents and lagomorphs so probably are accidental records for the lynx. Van Zyll de Jong (1966b) suggested that the scarcity of fleas on lynxes is linked to their habit of bedding on the trail and a lack of regularly used dens or burrows (with the exception of the nursing female). Hopkins (1960) described a louse (*Felicola spenceri*) from a lynx in British Columbia. In North America, seven cestodes (Adams, 1966; Bursey and Burt, 1970; Fyvie and Addison, 1979; Loewen, 1929; van Zyll de Jong, 1966b), two trematodes (Pearson, 1956; van Zyll de Jong, 1966b), seven nematodes (Pence et al., 1978; Rausch et al., 1956; van Zyll de Jong, 1966b), and one acanthocephalan (Schmidt, 1968) have been reported. Sadikhov (1952) described the nematode *Troglostrongylus assadovi* from *F. lynx* in Azerbaidzhan, USSR. Fagasinski (1961) reported the nematode *Toxocara cati* and the cestode *Taenia rileyi* from the lynx in Poland, but van Zyll de Jong (1963) questioned the identification of the cestode. Kazlauskas and Matuzevicius (1970) reported the cestodes *Taenia crassiceps*, *T. krabbei*, *T. pisiformis*, and *Hydatigera taeniaeformis*, and the nematode *Toxocara mystax* from the lynx in Lithuania. Diseases known to infect lynxes include panleucopenia, rabies, coccidiosis, and mycoplasmosis (Anpilogova and Sokov, 1973; Langford, 1974; Lewis, 1975; Povey and Davis, 1977; Matjuschkin, 1978).

Lynxes have been harvested for fur for over 2 centuries, but significant value (therefore trapping pressure) has developed more recently. The average price of lynx pelts in Canada rose from $38 (Canadian) to $216 between 1971 to 72 and 1975 to 76 (Brand and Keith, 1979). Increased harvest has been caused by price increases, but improved access to remote areas and the use of snowmobiles have increased trapper efficiency as well (Berrie, 1973).

Many of the studies about lynx have been conducted by tracking in the snow, telemetry on tagged individuals, and analysis of data obtained from carcasses. Berrie (1973) found lynxes were trapped most easily with a bait combination of grouse forms and beaver castor, producing one lynx per 74 trap nights. Leg-hold traps of various sizes commonly are used for capture (Berrie, 1973; Nellis et al., 1972; Saunders, 1963a). Immobilization has been accomplished with succinylcholine chloride at a dosage of 0.66 mg/kg of body mass, ketamine hydrochloride at a dosage of 15.0 mg/kg (Parker et al., 1983), and a phencyclidine hydrochloride called Sernylan (Berrie, 1973; Mech, 1980; Nellis et al., 1972). Berrie (1972) showed that males were more susceptible than females to comparable dosages, males being immobilized with 0.25 mg/kg Sernylan and females with 0.6 mg/kg. Mech (1980) immobilized lynxes with a combination of about 1 mg of phencyclidine hydrochloride and 0.5 mg of promazine hydrochloride per kg of body mass.

Harvest data may show a preponderance of males in younger age classes (Stewart, 1973), presumably because of dispersal, but sex ratios often approach equality when averaged over time (Brand and Keith, 1979; Parker et al., 1983). Yearly fluctuations in sex ratios reflect differential survivorship, phase of the cycle, and trapping sample biases. Kittens may be underrepresented in harvest samples (Berrie, 1973; Brand and Keith, 1979; Parker et al., 1983), possibly because of poor survival of kittens, trapping biases, and lack of maternal protection of yearlings.

Age can be estimated by examining ossification of epiphyseal plates of longbones (Nava, 1970; van Zyll de Jong, 1963), tooth replacement and cranial characteristics (Saunders, 1964), or cementum annuli (Nellis et al., 1972). Presence of an apical root foramen in canines of lynx less than 19 months of age aids in distinguishing kittens (Saunders, 1961). Grue and Jensen (1979) indicated that the first incremental line appeared in lynx canines between February and March of the second year.

Lynx populations should benefit through forest management favoring hares (Parker et al., 1983). *Eucalyptus* plantings in optimal habitat in Spain may be detrimental to lynxes (Valverde, 1957). Harvest during periods of low recruitment delays or suppresses natural increases in lynxes by leaving fewer lynxes in the breeding population. Suspending harvest for 3 to 4 years during low populations would result in greater overall harvest during population increases and higher numbers at the peak (Berrie, 1973; Brand and Keith, 1979). Shortened seasons would change the age structure of the harvest, because the proportion of kittens in the harvest increases through the season, whereas the proportion of yearlings decreases (Parker et al., 1983). When recruitment is high, a delayed season (January–February) would insure higher harvest of yearlings and lower harvest of kittens; orphaned kittens in the later season have increased chances of survival (Parker et al., 1983).

BEHAVIOR. Lynxes usually are solitary animals except for females with litters (Parker et al., 1983). They exhibit a strong reaction to the smell of the feces of conspecifics, to the sexual smell, and other strange olfactory and taste stimuli (Lindemann, 1955). Mutual avoidance may be effected through this mechanism, but during periods of prey scarcity mutual avoidance may cease to function as a spacing behavior (Brand et al., 1976).

During the breeding season, vocalizations become common. Purring and meowing is performed especially at dawn and twilight, but the loud bass meow of the male may be given throughout the night (Ognev, 1935). The call of the female is more of a vibrating whine (Guggisberg, 1975). Male lynxes display Flehmen, a behavior involving scenting or tasting of urine of the female followed by a stylized facial expression, to determine the reproductive condition of the female (Lindemann, 1955; Stehlík, 1979b). The period of receptivity lasts 1–2 days but preceding that time there is an increase in urine marking by both sexes (Stehlík, 1983b). Males hold on to the skin of the neck of the female during copulation (Stehlík, 1983b).

By tracking lynxes in snow, Saunders (1963a) found that kittens buried their feces and covered urination sites except when the crust of the snow was too hard. By late April, kittens had abandoned the habit. Adults commonly urinated and defecated along trails, sometimes in the same location (latrines), presumably to scent mark territories.

When several lynxes travel together (most commonly family groups), they follow in the footprints of the leader. Although lynxes generally avoid water, they can swim across large stretches if necessary (Ognev, 1935). Familiar features of the surroundings are strongly imprinted on the lynx. Orientation and homing abilities are effected primarily by visual means, and an excellent memory allows the lynx to locate pre-established hiding places (Lindemann, 1955).

Lynxes may feed at any time of day, but they are most active between dusk and dawn, and hide in rest areas during the day (Ognev, 1935; Saunders, 1963a). Lynxes stalk as close as possible to prey, then pounce on it in one or two bounds, or less commonly they leap down from a branch onto larger prey (Guggisberg, 1975). Prey are usually pursued 20–50 m, but chases have reached 100 m (Stehlík, 1979a). Tracking an adult female with two offspring in the snow, Saunders (1963b) found that the kittens often flanked the adult 15 to 40 paces when hunting through wooded areas. Upon entering clearings, they rejoined the female and frequently followed in her footprints. Lynxes often made hunting or resting beds in the proximity of recent hare activity. Kills were sometimes made from such beds. Barash (1971), Parker et al. (1983), and Saunders (1963b) noted instances of cooperative hunting.

When food is less limiting, lynxes may cache food for later use. Nellis and Keith (1968) trailed lynxes through snow and found that at least portions of 6 of 11 hares killed were cached, and six old caches were revisited. Berrie (1973), Haglund (1966), and Matjuschkin (1978) also reported caching by lynxes.

Hancock et al. (1976) reported an attack on a trapper carrying 12 hares. Usually attacks on humans are during periods of prey scarcity or when the human wears animal-hide clothing.

GENETICS. The diploid number is 38 chromosomes. The

autosomal complement includes two graded series (ranging from large to small) of eight pairs of metacentrics and eight pairs of the submetacentrics, and two pairs of medium-sized acrocentrics (Hsu and Benirschke, 1974). The X is a large submetacentric and the Y is a small submetacentric.

Kurtén (1968b) believed that the Scandinavian lynx population had a dual origin, from the south across Denmark and from the east through Finland. Mingling of immigrants from these origins resulted in the presence of character gradients in tooth size. Lynxes of southern Sweden seemingly were isolated at some time, indicated by a more narrow postorbital constriction than in other forms. Dilute mutation was observed in a lynx from Alaska (Schwarz, 1938). Jones (1923) described color phases, including "drab blue," "tabby," "light brown," and "fawn yellow." Ognev (1935) described an "ocher-orange" specimen.

REMARKS. Phylogenetic relationships within the Felidae are unclear. Kurtén and Rausch (1959) tentatively attributed differences between lynx crania from Alaska and Fennoscandia to clinal variation, initiating a move to consider these lynxes conspecific. Van den Brink (1970) concurred, but showed that the confluence of the anterior condyloid foramen with the posterior lacerate foramen, used to distinguish bobcats from lynxes in the Nearctic, also was present in *F. l. pardina* in the Palearctic, and referred the latter to *Lynx pardina*. Kratochvil (1975) suggested that bacular morphology could justify subfamilial classification of the lynx group and later (Kratochvil, 1982) added mathematical evaluation of karyotypes as support. Van Gelder (1977) argued that the ability to hybridize negated generic distinction of *Lynx* and *Felis*. Herrington (1983) examined the Felidae with cluster, principal component, and cladistic analyses, and concluded that the genus *Lynx* was a valid category within the Felidae. Stehlík (1979a) believed that behavioral differences justified *Lynx* as a genus. The current tendency in original research papers appears to be to accept *Lynx* as a genus, but acceptance is still not widespread. Should *Lynx* become the accepted generic designation, it is likely that the forms *lynx, canadensis,* and *pardina* will be elevated to species rank.

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